VOL. XXXIX No. 1 PSYCHOLOGICAL REVIEW PUBLICATIONS WHOLE NO. 177 1928

Psychological Monographs

Cerebral Destruction in Its Relation to Maze Learning

BY

NORMAN CAMERON

ASSISTANT PROFESSOR OF PSYCHOLOGY,
UNIVERSITY OF WISCONSIN

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the University of Michigan

1926

Published for The American Psychological Association by

PSYCHOLOGICAL REVIEW COMPANY

PRINCETON, N. J.
and ALBANY, N. Y.

TABLE OF CONTENTS

I. INTRODUCTION

In the early part of 1924 the writer made some preliminary experiments on the effects of destruction of the frontal poles of the rat cerebrum, repeating some of the early experiments but using instead of a simple two-choice apparatus, a series of complex patterns laid out on a universal adjustable maze. Unexpectedly, the results turned out to be quite the opposite of those found in the earlier work with the two-choice box. It seemed, therefore, worth while to make a systematic study along these lines. Following suggestions offered by Professor John F. Shepard, a plan of attack was adopted that has not only substantiated the findings of the preliminary work but has brought out some new phenomena of a rather interesting nature. The preliminary experiments, which are not included in this report, were carried out in the psychological laboratories of the University of Michigan. The experimental work that constitutes the basis for this paper was done in the comparative psychology laboratories established by the writer in the fall of 1924 at the University of Wisconsin. The general results of these latter experiments were given in an informal report at the Round Table Conference of Experimental Psychologists at Ithaca, N. Y., December 29, 1925.

The data included in this paper indicate the effects of destruction of cerebral tissue in the frontal regions of the rat's brain upon (*a*) the acquisition of a new habit, (*b*) the redintegration of an old one after a lapse of time, and (*c*) the capacity for adaptation to successive modifications of already-formed habits. A series of five different maze patterns was employed, and detailed records obtained on the behavior of thirty-six albino rats in a total of 8,553 trials.

The maze problem has in past years proved to be one of the most serviceable methods yet developed for gathering material for a study of learning and retention; and it seems likely to continue as an important means of increasing our knowledge of these

processes, in spite of the attacks that have been levelled at it by certain students of animal behavior. The writer believes that general statements concerning the parts of the central nervous system involved in maze learning based on the work of Franz and Lashley (1917) are decidedly premature. The subject, involving as it does an important laboratory technic, is of too great significance for the question to be settled so quickly. The conclusions these authors have arrived at apply only to their two-choice apparatus (fig. 1),—one that can hardly be called a " maze " in the ordinary sense of the word. So far as the writer can see, the results as stated in their papers were not intended by them to be taken as applying to the whole question of maze learning. But other writers have not been so cautious in drawing conclusions. Herrick (1926) in an excellent neurological interpretation of the work of Lashley and others, states in reviewing the experiments of Franz and Lashley that " the experiments described give no evidence of cortical participation at all in the formation and retention of a simple maze habit." Later, in referring to " simple maze learning," he says, " This case is very different from that of . . . the inclined plane latch-box which is related with the frontal regions." Now these statements are very misleading. The impression one gets is that simple maze learning is entirely subcortical and has no relation whatever to the frontal regions; and, in fact, the writer has already encountered this prejudice with regard to maze learning in several quarters. When one considers that the apparatus employed is not a maze at all, in the accepted use of the term, it can readily be seen that the results obtained should not be applied to the question of maze learning. Had a simple maze, with even as few as three or four cul-de-sacs, been used the results might have been very different. With the patterns employed in our own experiments, they certainly were. It may have been, as these authors appear to believe, that their problem was so simple as to make cortical participation unnecessary; but even this interpretation seems an unlikely one. Judging from his own results, the writer is rather of the opinion that the two-choice problem was such that differences in behavior between normal and operated-upon rats, although probably present, could not be

discerned by the observers because of the nature of the apparatus used and the simplicity of the adjustments that it forced. This will become plainer when the experimental data in this paper have been presented.

Opportunity is here taken to acknowledge the writer's indebtedness to those persons at the University of Michigan and at the University of Wisconsin who have contributed in one way or another to the success of the experiments reported in this paper. The writer desires to thank especially Professor John F. Shepard of the University of Michigan, who has helped him with advice and materials at all stages from the initial planning of the problem to the statistical treatment of the data obtained. The writer must, however, himself take full responsibility for the interpretations and the theoretical conclusions presented in this paper. Professor G. Carl Huber, Dean of the Graduate School at the University of Michigan, has been unstinting in giving his valuable time for consultation upon matters neurological. During the summer of 1925 he placed the facilities of a fully equipped laboratory of nervous anatomy at the writer's disposal. Professor G. C. Sellery, Dean of the College of Letters and Science at the University of Wisconsin, has generously assisted by assigning funds for the purchase of apparatus and materials.

II. REVIEW OF THE LITERATURE

The relation of the cerebral cortex to the acquisition of new habits and the retention of old ones is of the utmost importance to general psychological theory. It is therefore remarkable that one finds such a dearth of experimental data on the problem. With the exception of some practically uncontrolled observations made by physiologists in the course of their work on decerebration, no reliable material appears in the experimental literature until 1912, when Burnett's report on the effects of decerebration of frogs upon their reactions in a Yerkes maze appears. From his failure to force the necessary associations Burnett concludes that in the absence of cerebrum, learning is impossible. On the other hand, results originally obtained by Yerkes (1903) on normal animals might lead one to suspect that the task set was not a simple one for a frog. Hence, while Burnett has clearly demonstrated the inability of a brainless frog to learn this apparatus, he has not established his claim that all learning, whatever its nature, necessarily involves the cerebrum.

Franz and Lashley (1917) experimented upon the effects of cerebral lesions on learning in the albino rat. These authors were interested primarily in the question as to whether or not removal of certain parts of cortex would produce any demonstrable change of behavior in a maze. A very simple system of three alleys (fig. 1) was used in which the animals were required to go from the starting compartment *a,* along the central alley *b* to the food at point *e* in the alley *d,* and not into the alley *c.* As the habit involved was extremely simple, the criterion used was largely that of the general behavior of the rat upon being released from the starting compartment and just before. Fifteen trials were given per day in the learning series. After the learning was "complete," the criterion selected being that of ten consecutive errorless trials, the rats were operated upon by passing a sharp instrument diagonally through trephine openings in the skull, in the neighborhood of the coronal suture, and drawing the instru-

ment to the sides of the cranial cavity. No attempt was made to remove the part thus severed from the cerebrum. Within forty-eight hours after the operation, each rat was given a test series of fifteen runs in the two-choice apparatus and time and error records taken. These results were then compared with those

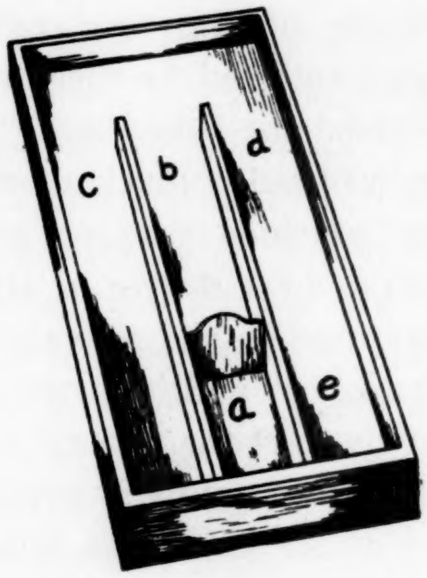


FIG. 1.

LASHLEY'S SIMPLE MAZE.

obtained in the first trials of the learning series in order to arrive at a measure of the degree of retention of the habit. With the exception of one animal that was so inactive as to make no attempt at all, the rats gave evidence of good retention of the habit after frontal destruction. Animals that had been overtrained lessened their running time by 87 per cent and the number of their errors by 90 per cent; those that had not been overtrained bettered their time record for the first fifteen trials by 29 per cent and their error record by 53 per cent. The authors report the general behavior of the rats in the apparatus as indicating in all cases familiarity with it. Postmortem examination of the brains is deferred to a later paper.

Franz and Lashley conclude, on the basis of the foregoing results, that in the white rat (1) learned reactions are not greatly interfered with by removal of large portions of the frontal regions of the cerebral cortex, and that (2) the possibility of this habit's being entirely subcortical is suggested by the results.

In a subsequent report (Lashley and Franz, 1917) an attempt is made to correlate the behavior findings given in the preceding paper with the nature and extent of cortical destruction as indicated by the autopsies. Difficulties arising in the microtechnic, using the toluidin blue method, resulted in the total loss of two brains and the damaging of most of the remainder. A composite picture based on an estimate of the total extent of surgical injuries to the cortex cerebri suffered by these animals was presented. The authors expressed the belief that " in every case it is probable that the lesion affected a much more extensive area than is indicated." They conclude that no correlation exists between the extent of lesion and the degree of retention. Before being killed, six of the rats used in the above experiments were subjected to a second operation in which cortex in other regions was destroyed. In spite of the fact that a total (composite) area constituting half the entire cortical area was involved in the three survivors, perfect retention of the habit was demonstrated. The authors consider that they are entirely justified in assuming *" that the functioning of the maze-habit is independent of the frontal region of the cortex,"* a conclusion that is exactly the opposite of that arrived at in our own experiments.

Lashley (1920) finds that destruction of the frontal region of cerebral cortex results in an increase in general activity as measured by a modified Slonaker apparatus. This conclusion seems to be in agreement with the general observations that have been made upon various animals after injury to the frontal region. Herrick (1924; 1926), in two excellent monographs on the functional side of comparative neurology, outlines the phylogenetic development of cortical and subcortical structures, and in the latter work attempts to correlate these with the findings of Lashley and others. The writer is especially indebted to the theoretical interpretations placed upon the experiments reviewed. His objections to those that are out of harmony with the results of the experiments reported in this paper have already been voiced in the *Introduction.* The section following this will describe the apparatus and the procedure, after which the results of this investigation will be presented.

III. APPARATUS AND METHODS

1. The Mazes

Five different maze patterns were used in all. These patterns were laid out on a universal adjustable maze copied from one originally designed by Professor J. F. Shepard for the University of Michigan laboratories. In view of the fact that this maze has turned out to be the most serviceable developed for all-around laboratory work, the liberty is taken of supplementing here the very brief description given by Shepard (1921). The Michigan maze is made to accommodate mammals as large as monkeys and small dogs. That used in the experiments forming the basis for this paper is an exact replica of the Shepard universal type on a much smaller scale, intended specifically for use in the ordinary animal behavior laboratory where space is limited. The dimensions given below as worked out by the writer apply to this reduced model.

The base is a single piece of ¾″ hard wood measuring 64″ x 64″, and reinforced with wood cleats to raise it off the floor and to prevent warping. Holes ½″ square are sunk to a depth of ⅜″ in the base in rows of 16 x 16, each hole 4″ distant from the next. The entire base is painted a battleship gray with washable paint rubbed to a dull finish. Two hundred and fifty-six wooden posts each 8″ long and ½″ square are prepared with a lengthwise slit in each of their four faces $^{9}/_{64}$″ deep and $^{3}/_{64}$″ wide. Extra posts are kept on hand to replace those accidentally split. Three hundred plates of galvanized iron, No. 24 U. S. gauge, are cut 8″ long and 3¾″ wide.

When the posts are placed in an upright position by driving them into the holes in the base, the variety of patterns that may be laid out from previously prepared drawings by means of the galvanized plates is practically unlimited. All alleys then measure 4″ across. Doors for the starting box and for the food box are

provided by soldering a galvanized plate to two small brass hinges which are then screwed to a post. A hole is bored in the free upper corner of the plate and two strings attached. The strings are passed from the door to the chair in which the experimenter sits, so that he may be able readily to open or close either one without appearing on the scene. The apparatus is illuminated by four 100-watt lamps symmetrically placed six feet above the floor of the maze. The entire maze is covered by a wire screen of 2 x 1″ mesh which is fastened to the base at the sides by means of cords tied to strong staples. A close-mesh cheese cloth screen mounted on a wooden frame surrounds the apparatus and conceals the experimenter and the laboratory from the animal in the maze.

The maze patterns used in this series of experiments were five in number. The rats were divided into four groups and two of the groups run through all five patterns successively, while the

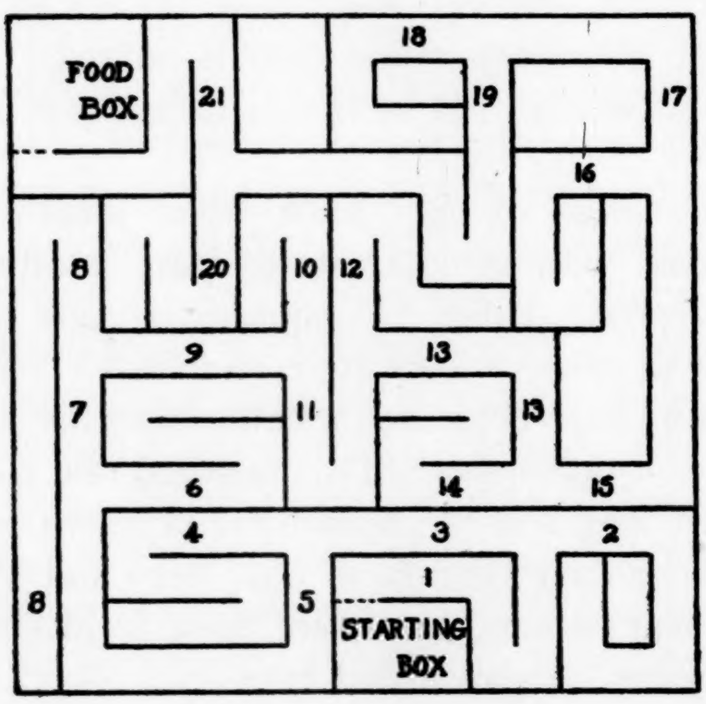


FIG. 2. PATTERN OF MAZE I.

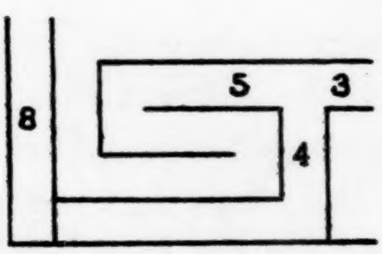


FIG. 3. MODIFICATION OF I TO MAKE MAZE Ia.

other two were run through three only. The first maze problem (fig. 2) was followed by one in which there is a modification

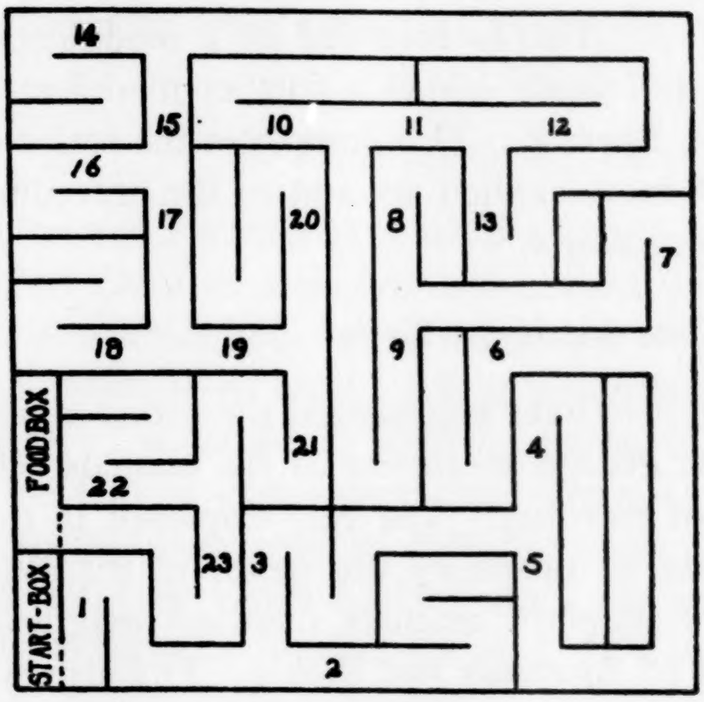


FIG. 4. PATTERN OF MAZE II.

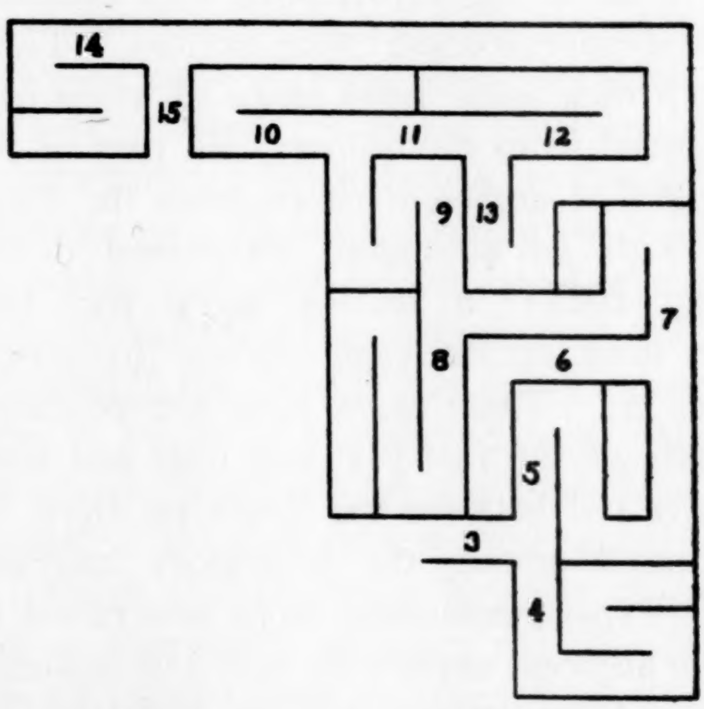


FIG. 5. MODIFICATION OF II TO MAKE MAZE II a.

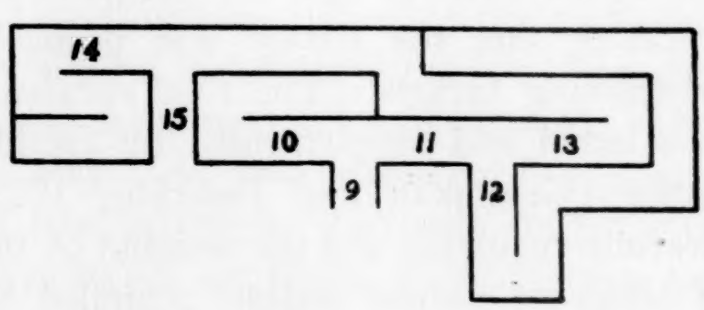


FIG. 6. MODIFICATION OF II a TO MAKE MAZE II b.

of one block of alleys as indicated in figure 3. The third pattern used (fig. 4) is quite different from either Maze I or its modification Ia. After an interval, the third pattern, Maze II, is repeated as a retention test. This is followed by a modification as indicated in figure 5; and finally comes a further modification of Maze II as depicted in figure 6. This completes the series of problems set the rats. A more explicit account of the procedure, experimental and surgical, follows.

2. The Animals Used

Various workers in the field have emphasized the prime importance of standardizing the general treatment of the animals used in psychological studies of learning. The rats employed in this series of experiments were all raised by the writer in the Wisconsin laboratories from standard animals obtained originally from the Wistar Institute of Anatomy and Biology, Philadelphia, Pa. They were housed in metal cages furnished with excelsior bedding over a galvanized narrow-mesh wire bottom. These cages are all mounted on a rack made from strips of angle iron bolted together and suspended from the ceiling. No part of the rack reaches below a height of eighteen inches from the floor. Each cage is equipped with an automatic water-feed device (Greenman and Duhring, 1923); a shallow metal tray two inches beneath the mesh floor of the cage catches droppings, urine, water, spilled food, etc. These cages have proved clean, dry and healthful. In spite of the fact that wild rats and mice are in the laboratory walls and between the floors no signs of parasites have ever appeared among the laboratory animals. During the course of these experiments some stock rats raised in exactly the same manner in adjacent cages were killed by students of parasitology and examined for external and internal parasites but without success, indicating that the colony was probably entirely free from such disturbing factors. The food consisted of table scraps carefully selected and supplemented by freshly cooked McCollum's mixture (Greenman and Duhring, 1923, p. 55). This diet was carefully regulated and the weights of the animals checked up with tables of normal weight compiled by

Donaldson (1924). After several months of continuous experimentation all rats were found to be in excellent condition as regards general appearance of coat, face, etc., and their activity and curiosity were typical of the healthy rodent "athlete."

3. Experimental Procedure

After some preliminary trials with stock rats, both normal and surgical cases, a standardized method was adopted and rigidly followed throughout all of the series. This will be discussed in some detail, since results are so often dependent upon the maintenance of a certain invariable routine for all animals alike and at all stages of experimentation. Routine treatment forms a sort of general background of fairly constant stimulation patterns and consequent responses against which the specific changes involved in the actual experimentation may stand out clearly. Description of the routine method follows.

Each rat was fed in the food box of its first maze for fifteen minutes on each of three days preceding that on which it was scheduled to start. A recent investigation by Warden (1925) has demonstrated beyond question the importance of this phase of laboratory method in reducing the feeding-exploring activity, thus saving time and helping to eliminate emotional and other disturbing variables from the results. On the fourth day the rat was placed in the starting box and the door opened by the experimenter by means of an attached cord. As the rat passed into the maze proper the stop-watch was started, and as soon as the animal was clear of the door it was gently closed after him. As the rat ran through the alleyways its path was recorded by means of numbers previously assigned to them; partial entrances into cul-de-sacs and points of reversal on the true path were designated by fractions, following the method developed by Shepard. After the rat had entered the food box the door was shut behind him and the stop-watch was stopped. The rat was permitted to eat a very small cube of cooked liver that had been placed in the food box before the run was started. On its last run it was allowed to eat for two or three minutes before being removed to

the cage. The remainder of its daily ration was given it in the home cage, as it was found to be impracticable with such a large number of rats to allow them sufficient time for a complete meal in the maze. Left to themselves rats will not normally finish their daily ration in a short time; on the contrary, they intersperse their nibblings with exploratory sniffing, running and occasional hopping about the cage. Our method was therefore in line with the animals' natural feeding activities.

Only one trial was permitted on the first day of running. On the second day the rat was required to make three trips through the maze, a liver cube being awarded at the end of each trip. On the third day of running a total of six trips was required. From then on six trips were made by the rat daily until the pattern was adjudged learned. Learning was arbitrarily considered as "perfect" when five consecutive errorless runs had been made on a given day. Entrance into a cul-de-sac of about one-third of the animal's head was counted as an error. If the rat turned about and retraced its steps it was credited with an error, and each entrance into a cul-de-sac on the way back was counted as an error also.

After a given rat had learned a maze "perfectly," it was placed each day of the no-practice period in a large enclosed space on the floor for fifteen minutes. A little food was scattered about so that the animal would be given some incentive to keep "on the move." This procedure was followed to meet the criticisms of some authors that no attempt is usually made to keep the animals in good running condition during the period of no-practice (*e.g.*, Watson, 1914). When the no-practice period had expired the regular maze-running procedure was repeated exactly as before, beginning with one trial on the first day, three on the second, and six on each day thereafter until the maze was mastered.

The thirty-six rats were divided up into four groups. The specific procedure for each group was somewhat different; hence, it becomes necessary to describe each method separately.

Group A—Each rat in this group was run through Maze I until learning was "perfect," in the sense given above to the

word. Running was then discontinued for a period of six days during which time the rat was exercised for fifteen minutes daily in the enclosure at about the hour when it would ordinarily be threading the maze. On the seventh day after its last run in Maze I, the rat was begun in Maze Ia following the standardized procedure outlined above. On the seventh day following the last run in Maze Ia each rat was started in Maze II. After Maze II had been mastered a period of six days was allowed to elapse, as was done between I and Ia and between Ia and II, and on the seventh day each rat was operated upon in a manner later to be described. A period of thirteen days was now permitted to elapse after the operation and on the fourteenth day each animal was introduced again into Maze II, as a test of retention. On each of the first seven days following the operation the rats were not regularly exercised in the enclosure but instead were removed one by one from their cages and placed upon an observation table, where they were permitted to run about while the writer carefully observed them for any disturbances of general behavior. Any abnormality of posture, gait, etc., was recorded on the spot. Some of these observations will be given in the *Case Reports,* following the description of the operation.

On days eight to thirteen inclusive after the operation the rats were exercised as before in the enclosure after first having been examined each day for abnormal behavior. On the fourteenth day following the operation, that being the twenty-first day after the last run had been made in Maze II, the retention test in the same maze was begun. When this maze had been thoroughly re-learned, the usual six days of no-practice elapsed, with routine exercise each day, and then Maze IIa was begun; the same procedure was followed during the no-practice period between Mazes IIa and IIb. Completion of Maze IIb concluded the behavior part of the problem. The beautiful condition of the rats at the end of the problem and for some time thereafter, up to the point where they were sacrificed for the microscopic study, indicates that no general pathological consequences were suffered as a result of the operations. It was quite impossible to detect the difference between normal and surgical cases after the incisions

had healed without examination of the ears for number holes, or the scalp for scar tissue.

Group B—The rats in this group were not run through Mazes I and Ia at all; and they were operated upon before they had been used in any experiments whatever. The procedure was to take these animals and operate upon them first, after which they were treated in every respect the same as those in group A. That is, on the fourteenth day following the operation they were begun with Maze II, and after this had been successfully learned they were given the routine six days of no-practice and started in Maze IIa on the seventh day; after IIa had been mastered six days were allowed to elapse, and then Maze IIb was learned. The general appearance and behavior of these animals were in every respect identical with the appearance and behavior of the rats in group A. Group B is intended as a control on group A for the purpose of determining whether or not there was any retention of the habit after the operation in the case of the latter group. Thus, if the rats of group B were to make as good a showing on the average as those of group A, one might say that very little if any of the effects of previous training had remained after the operations. While should the case turn out to be the opposite, and group A were to make a noticeably better record than B, one would be justified in assuming that the effects of previous training had to some extent survived the surgical treatment.

Group C—This group of rats was treated in every respect the same as was group A, excepting that its members were not subjected to the operations. Following their initial learning of Maze II they were given a three weeks vacation before being returned to this maze pattern for the retention test. During no-practice periods, and in fact at all times, they were put through the same routine as were group A rats. Group C thus constitutes a normal control for comparison with the surgically treated rats of A. Such a comparison should furnish the basis for a rough measure of the effects of the operations upon retention of a past habit and upon the capacity for adaptation to modifications of this habit.

Group D—The rats in group D were subjected to the same conditions as were those in B, excepting that no operation

was performed upon them. They thus acted as normal controls for comparison with group B in the same way that those of C served as controls on group A.

Summary—A brief restatement of the material in this section, expressed somewhat differently, may help to bring out the purpose of each group in the general problem more clearly. Rats in groups A and C were run through all five maze patterns in the order I, Ia, II (pre-retention), II (post-retention), IIa, and IIb. Six days of no-practice were allowed to elapse between the different maze patterns. Between the completion of learning of Maze II and the retention test in the same maze, however, a period of twenty days was permitted to pass by, during which rats in group A were operated upon while those in group C were not. Thus C represented the normal behavior and A served to indicate the effects of cerebral lesions.

Rats in groups B and D did their very first work with Maze II, after which IIa and IIb were run with the usual intervals between. Animals in group B were operated upon two weeks before being started in their first maze problem; those in group D were not operated upon at all. These two groups thus stand in the same relation to each other as do the above pair of groups to each other. The operative procedure in both instances is the only difference in the treatment given the members of each pair of groups.

An intercomparison between groups A and B is also desirable for the following reasons. Differences brought out in the comparison of group A with group C, while giving a measure of relative retention in the two groups, would not show whether all retention was absent in the case of group A or only part. Maze II is an entirely new problem for group B while group A has already learned it on a previous occasion. A better record for group A would therefore indicate retention to at least some degree. The degree of retention would be indicated by the comparison between groups A and C suggested above.

Similar comparisons can be made with respect to the effects of the cerebral lesions on the ability to adapt to modifications of already established maze habits by a study of the records for Mazes IIa and IIb.

4. Surgical Procedure

All operations were carried out in a small room reserved exclusively for the purpose. This room was situated some sixty feet from the vivarium, as it was deemed advisable to prevent the ether from reaching the other animals during the week of operating.

Each rat was placed under a bell-jar having a stoppered opening near the bottom. Pure anaesthetic ether was then poured in through the opening on to a small quantity of absorbent cotton previously pushed in through the hole. After the rat had become completely motionless it was tied by means of silk fish-line ventral side down on a standard animal board made to scale and covered with thick cotton pads. During the entire operative procedure the rat was kept under the anaesthetic by frequent applications of ether-soaked cotton.

After the long hair on the dorsum of the head had been removed with scissors, a depilatory was applied and left on for several minutes. This was then washed off with a 1/1000 solution of bichloride of mercury, and a cotton pad soaked in this solution was left on the shaven scalp until the incision was to be made. Surgeon's gloves previously sterilized in an autoclave were then donned by the writer, and sterilized instruments were spread out by an assistant who handled the instrument tray with sterile forceps.

The incision was made down the mid-dorsal line of the scalp with a small scalpel. An area of skull was laid bare extending from the anterior border of the palpebral fissure to the caudal border of the interparietal, and laterally on each side to the line of insertion of the face muscles. The scalp flaps were held down by attaching to their borders eight very small haemostats. Next a small hole was very slowly and carefully drilled in the skull on either side of the sagittal suture, just rostral to the coronal suture. A sharp cataract knife was then inserted successively into each hole obliquely down and forward, and drawn carefully from side to side within the cranial cavity. After the knife had been withdrawn and the hemorrhage stopped, the scalp was sewn together

again with surgeon's silk. A cotton and collodion dressing was next applied, and the animal removed from the operating table and gently laid in a clean cage containing fresh excelsior, water, and a little food. Speed of recovery from the immediate effects varied somewhat from rat to rat, but in all cases except one attempts to eat were made within the first hour after removal from the operating table. The general after-effects are given in the next section.

IV. RESULTS OF THE OPERATIONS

1. Case Reports

In this section one complete record of an operation and its general consequences will be transcribed from the laboratory notes taken at the time; in the case of the remainder of the animals only significant behavior after the operation will be given.

a. *Complete Case Report on Number Six*

Rat number six is selected for two reasons, *viz.,* it was the first animal to be operated upon in this series of experiments, and the notes for it are the most complete. The laboratory report made by the assistant during the operation follows:

April 22

10:12—Rat under bell-jar.
10:32—Tied on animal board.
10:58—Depilation complete.
10:59—Scalp cleaned—bichloride of mercury, 1/1000 solution.
11:00—Cotton compress bichloride of mercury on scalp, covering depilated area.
11:02—Incision begun occipital area; longitudinal incision extending to anterior margin of eyes; haemostats applied.
11:05—Underlying fascia separated.
11:10—Operating area cleaned.
11:13—Opening being made in skull on each side of sinus, rostral to coronal suture.
11:24—Cataract knife inserted diagonally toward anterior, and arc described within cranium. Rather profuse hemorrhage from right side which very soon stopped of its own accord.
11:30—Haemostats removed.
11:32—Four stitches taken in scalp.
11:42—Collodion applied to wound.
11:45—Cotton and collodion dressing completed.
11:48—Removed to clean cage.

After one hour, apparently in stupor; maintained crouched attitude with occasional shift in position. Attempted to eat when food placed in dish before it. Apparently unable to get head over edge of dish. (Height of edge about one inch.)

April 23

Placed on table for observation. Very cautious; body held close against the ground; stiffness of left hind limb; usual sniffing and exploratory movements at

edge of table. Shakes head occasionally as if wet. Vibrissae active. Frequently stands up on hind legs when front feet encounter vertical surfaces. Tilts head slightly down on right side. Washing movements about head and face slow and don't reach very far back. General condition very active. Appetite good. When in cage, picks up food and retreats to rear of cage as normal.

April 26

Behavior apparently perfectly normal. Animal very active; sniffs, waves vibrissae and head; position of legs, feet, tail normal; general bodily orientation normal; tame; can be handled as before operation.

After this nothing of interest is reported in the notes excepting that upon being put into a cage with number ten, the two fought (both females) so constantly that it was deemed safest to protect all the material by keeping each rat in a separate cage. Notes on general behavior in the maze, taken independently at the same time that records of the run were being made by the assistant, follow.

Maze: May 6

Left door without preliminary sniffing; movements quite normal; shakes head occasionally; frequent sniffing in maze; long stuporous pause (eight seconds) in last cul-de-sac; much sniffing in food box.

Maze: May 7

Movements quick; often retraces with very "decided" appearance; normal in general behavior. On second trial, much sniffing at door of starting box when opened; then went off like a shot. Third trial, same as second; before leaving attempted to nibble experimenter's hand; much sniffing in maze; scratching head at number seven cul-de-sac.

Nothing further of any note is recorded.

b. *Significant Notes Taken on Other Animals*

Number Two—This rat showed a very persistent tendency for the first four days after operation to hang over the edge of the table with its head, front paws, and a large part of its trunk suspended in space. It also showed some general disturbances of locomotion. A few lines of notes follow: "Attempts to hang over table to point where hind feet slip; locomotion very unsteady; running stiff yet fairly rapid." Next day: "Requires continual watching; always in danger of falling over edge. (Later). Pulled back on to table by experimenter as losing

balance. Movements rapid and jerky; gait waddling; tendency for feet to spread." Third day after operation: "Spends all time hanging over edge; if placed in middle runs immediately back to edge." (The rat was on a table seven feet long by eighteen inches wide; but it never ran lengthwise on it; hence, the running to the edge could not have been merely a matter of accident.) "Gait and posture normal; very active." Fourth day: "Tendency to hang over edge, but not so marked." This tendency was almost absent on the fifth day, and had entirely disappeared on the sixth. The rat was otherwise quite normal. Its maze running disclosed no noticeable abnormalities of general behavior.

Number Four—Nothing very unusual was observed in the case of this rat. It showed a rather marked tendency to run with its head tilted down on the right side, which tendency disappeared on the fifth day after operation. Its movements were unusually jerky and cautious during this same period. On the second day a very definite fear response was elicited when the animal came suddenly upon a vertically placed board at one end of the observation table. Notes on maze behavior read: "Ran out quickly; movements almost automatic. Behavior perfectly normal."

Number Six—(Given in detail above.) On the first day showed the same tendency as did number four to tilt the head down on the right side. Its left hind leg was stiff; and it shook its head "as if wet" indicating probably some sort of irritation due to bandage, etc. By the fourth day all the symptoms reported above had disappeared. The maze behavior has already been given in the detailed case report.

Number Seven—This animal is especially interesting because of the remarkably poor record it made in the retention series, when it took 231 trials to relearn Maze II which it had completed three weeks previously in 34 trials. The scalp incision was made at 10:37 and the cataract knife inserted into the cerebrum at 10:48. Nothing eventful is recorded excepting that at 10:56 during the stitching of the scalp rather marked spastic movements occurred. Stitching was stopped but the movements recurred irregularly even when the animal was not being touched.

The report for the third day after the operation reads: " Runs with nose very close against surface; very active; gait normal but very slow." The general activity was less on the fourth and fifth days, and a very slight tendency developed for the head to tilt downward on the left side. As some very peculiar behavior appeared later, the day to day report is given below in an abbreviated form:

Day 6—" Moderate activity; slight tilt of head toward left; back legs run stiffly; movements rather slow."
Day 7—" Moderate activity; no tilt of head; abdomen held low; slight tendency toward 'Chaplin feet' in locomotion."
Day 8—" Quite active; gait and posture normal."
Day 9—" Very active; much scratching and washing; peculiar crouching and backing behavior; normal in other respects."
Day 10—" Same crouching and backing; urinated on table; normal in every other way."
Day 11—"As above."
Day 12—" Same crouching and backing; fell from table; leaped into air and squeaked when attempt was made to pick it up; urinated on table; general behavior otherwise fairly normal; quite active."

In the maze it acted at the start as though it were in a totally new situation. There were returns, sniffing about, hesitations, etc. The general behavior was otherwise normal. The records show that while it took an almost interminable time to relearn the maze, the number of errors made indicated some effects of previous training.

Number Nine—This animal showed the same tendency evinced by number two to spend all its time at the edge of the table. It did not usually lean over the side to such an alarming degree as number two, but on the seventh day it suddenly fell from the table to the floor. The only difference in behavior following this accident was that of resisting removal from the home cage. The animal's gait was markedly waddling up to the twelfth day, and a tendency to what is described in the laboratory notes as " Chaplin feet " was observed. (The term " Chaplin feet " refers to a gait in which the large hind feet of the rat are thrown out laterally in an exaggerated manner, strongly suggestive of the great film comedian's walk.) General movements were slow; activity varied but was never above moderate. A very strong tendency to urinate frequently and copiously during

observation was recorded. Urination in the maze occurred on the first day, but not thereafter; behavior in the maze was normal although movements were at first rather slow.

Number Ten—General behavior is reported as "very active." Locomotion was at first slightly waddling, with the belly held about five millimeters above the surface of the table. On the fifth day the animal's breathing is recorded as "extremely rapid and shallow; movements jerky; a little nervous." On the second day of maze running it suddenly, without apparent reason, whirled completely about.

Number Eleven—This rat's behavior was noteworthy because of its frequent urination during examination and its almost continual sniffing. On the first day after the operation its foot movements were very exaggerated. Each front foot was put down very deliberately; the hind feet were turned out markedly in walking—"Chaplin feet." Associated with the sniffing were frequent protracted stops followed by jerky movements forward. General activity throughout the observations was moderate.

Number Seventeen—Frequent urination at first was a prominent feature of this rat's behavior. A downward tilt of the right side of the head was present on the second day, but had disappeared by the third. The animal progressed rather slowly; the maze-running had begun before the rat appeared normal. General activity throughout was moderate. On the first day of maze work, opening of the door resulted only in a long pause on the part of the rat, followed by a great deal of sniffing and a very cautious exit. The behavior was very much like that of a rat never before in a maze; yet, while it took longer to relearn than originally to learn Maze II, it made a much better record of errors in the first few trials after the operation than before. After its first exit from the starting box into the maze proper, there was a decided effort to return which was prevented by the closed door.

Number Twenty—The head showed a tendency to tilt downward on the right side until the tenth day after operation. The animal was very active all the time, sometimes hyperactive. Its movements were so very swift that on the second day it fell from

the table twice in succession, but was caught both times two or three inches below the table top. On the first day it showed great general excitement with attempts to leave the table. On the fourth day it fell completely from the table to the floor, but no harmful effects were apparent; in fact, this rat learned Maze II before any of the others of its group. There was steady improvement until by the seventh day it was normal in all respects excepting that of the tilt to the right.

Number Twenty-one—When the cataract knife was inserted, this animal bled profusely on the right side; otherwise the operation was uneventful. A slight lean toward the left was observed up to the fifth day. The abdomen was held very low and the feet outspread until the sixth day. Otherwise its locomotion was almost normal from the start, and its activity normal from the second day on.

Number Twenty-two—A slight lean of the head toward the left. Movements were at first slow; the hind feet were spread apart and the front ones rather deliberately placed on the table. Activity increased steadily from below normal to above normal by the fourth day. After this, behavior was quite normal in every respect.

Number Twenty-three—A severe hemorrhage followed cerebral incision. After the operation, there was a marked tendency on the first two days for the rat to hang over the edge of the table to the danger point. While its movements were very slow on the first three days, its general activity was good and its gait and posture normal from the very start. It showed the same tendency toward frequent and copious urination evinced by numbers nine, eleven and seventeen. This disappeared soon after maze-running was begun.

Number Twenty-four—A very marked tendency to lean over the edge of the table, as with numbers two, nine and twenty-three. Removal from the edge was invariably followed by a prompt return to it. Beyond a slight tendency to tilt the head downward on the left side, the animal's behavior was normal and its activity good.

Number Twenty-five—The most prominent abnormality was that of constant sniffing, in which behavior it exceeded even number eleven. During the first two days it also exhibited the tendency to lean over the edge of the table. This was combined with very frequent washing movements and shaking of the head, possibly due to bandage irritation. The snout was often thrown upward during running. By the fifth day behavior was quite normal, excepting for the continual sniffing which continued on into the maze-running.

c. *Concluding Remarks*

This completes the report on the general behavior of the animals after the operations. For the records of the groups in the maze-running, the reader is referred to the section below entitled *Experimental Results.* It must not be assumed that any differences noted between the behavior in the maze of rats in group A and those in group B are due to differences in surgical technic. The rats were, in fact, not operated upon in numerical order; nor was one group operated upon before the other group. The actual order in which they were laid on the operating table was 6, 10, 7, 9, 21, 17, 2, 24, 4, 20, 22, 11, 3, 23, 25. Only one death occurred as a result, directly or indirectly, of the operations. Rat number three came out from under the anaesthetic while the scalp was being stitched up. The struggling that ensued, although of but a few seconds' duration, resulting in a very severe hemorrhage which the writer thought he had checked before the dressing was applied. Fifteen minutes after the animal was placed in his cage, however, it was found to be dead and examination of the bandages indicated that death was due to bleeding. The conditions of the experiments demanded that the animals be kept alive for a period of nearly three months after the operation. It may be said that within a few weeks there was no observable difference either in the appearance or the general behavior of those that had been operated upon and those that had not. The former seemed in every respect as reactive to their general surroundings as did those of the normal control groups. A report on the microscopic findings follows.

2. Microscopic Examinations

Almost three months after the operations the rats were killed and their brains removed for microscopic study. It was originally intended to stain the brain tissue by a modification of the Weigert-Pal method. The choice of method was a very unfortunate one, for the process involved necessitated the use as a mordant of a solution containing potassium bichromate. Now material that has been subjected to a chromate treatment is almost always more or less refractory because of difficulties in dehydration and consequent troubles in the sectioning. The neurological tissue prepared in the course of this study was certainly no exception. Dehydration was apparently incomplete and as a result the tissue became so brittle that the utmost care in sectioning did not prevent the loss of the greater part of the material. It was only through the advice and example of Professor G. Carl Huber of the University of Michigan that enough was saved to be able to demonstrate the existence and position of lesions in certain cases. While more material might have thrown additional light on the relation between cerebral physiology and learning, the nature of this investigation demands only that the fact of cerebral lesions in the frontal region be established. For, the behavior results undeniably controvert the misconceptions that have arisen through the statement of former workers, quoted in the *Review of the Literature,* " that the functioning of the maze-habit is independent of the frontal region of the cortex."

The microscopic evidence for the presence of lesions in the frontal region of cortex in some of the experimental material is presented in figures 7 to 12 inclusive. The outlines and the location and extent of the lesions were sketched in under low power with the aid of a Leitz drawing ocular, which has a somewhat larger field than the ordinary camera lucida. The lesions themselves were then studied under higher magnification and the exact nature of them reproduced as well as possible with the pen. Figures 7 to 10 represent sections from rat number nine. Their distances from the frontal poles are estimated respectively at 400, 600, 1,000, and 1,200 micra. Figure eleven represents a

section from rat number ten. Its position is difficult to determine as the sections before it were almost all lost in the staining and sectioning. Figure 12 is of a section from rat number seventeen taken at a distance from the frontal poles of about 1,400 micra.

In figure 7 the left side shows almost one-half the hemisphere separated from the main body of the brain. The connection

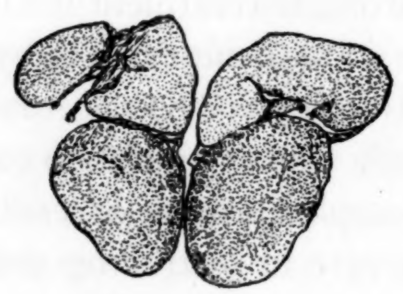


FIG. 7.

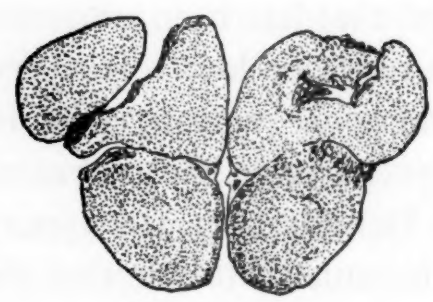


FIG. 8.

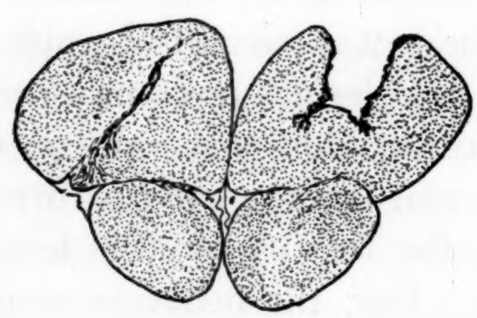


FIG. 9.

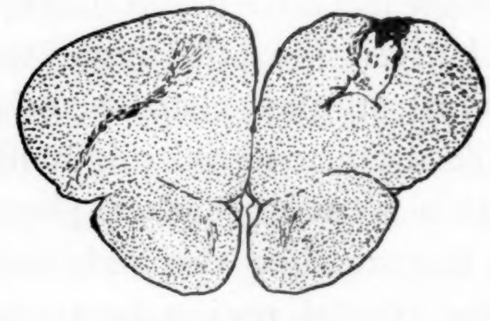


FIG. 10.

FIG. 11.

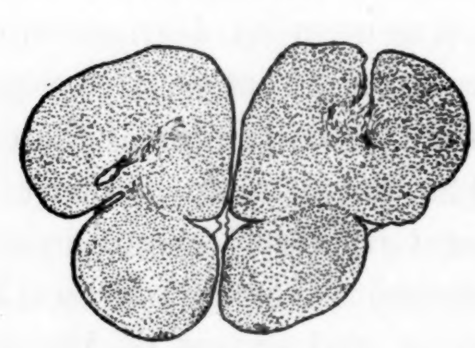


FIG. 12.

consists of a large number of coarse strands of non-nervous tissue, giving anatomical continuity of a certain order but certainly no functional continuity. A healed lesion appears running medially a little way into the body of the cerebrum. On the right side, there is a considerable lesion running mediolaterally across

the section, extending medially nearly to the surface. In the next section (fig. 8) the two parts of the left side are almost severed. Where they are joined, however, the fibrous strands are denser and more organized; that is, they all run in the same general direction and form real anatomical continuity between the main body and the partly severed portion. Under high magnification there is no evidence of any nervous tissue extending from one portion to the other. The appearance is that of a completely healed lesion composed entirely of coarse, densely intertwined fibrous strands with cell-bodies here and there. The right side shows a ventrally-directed lesion separating the upper part of the cerebrum into two unequal parts, and extending medially as a Y-shaped projection into the cerebral tissue. A crescentic area of lightly staining tissue, somewhat areolar in appearance, caps the forks of the Y. Dense fibrous tissue borders the lower fork and part of the vertical fissure of the lesion.

The left side of figure 9 shows practically as great a division between the two portions as does that in the preceding figure; but the two parts are not spatially separated. The lesion appears as an oblique, dorsoventrally directed line of coarse fibers which separate to leave two small spaces near the center and fan out toward the ventral border. On the other hand, the right side shows a complete separation of tissue to form a large bay which sends a ventromedial and a ventrolateral estuary from its floor into the cerebral tissue. Fibers appear here and there along the borders of the lesion. Figure 10 presents very much the same general appearance. The lesion on the left side is difficult to make out under low magnification, but can be followed readily in the central portion under high power. Toward the periphery in both directions it fades into the surrounding tissue. On the right side it is quite as clearly marked as in the preceding section. Dense tissue caps it on the dorsal aspect and dense strands extend mediolaterally from the floor of the cavity.

The section depicted in figure 11 shows an irregular cavity filled with very lightly staining material containing fine fibers, with a few clear spaces. Densely staining fibers are indicated in the drawing. The right side shows no injury. Its small size is

due to the angle at which the sections in this series were cut. The section in figure 12 shows a ventrally located lesion on the left side with a sharply defined cavity at its ventromedial extremity and a less clearly marked lightly staining elliptical area extending upward from it. Examination of subsequent sections in this series reveals a passing upward of this lesion until it breaks through at the surface about 400 micra back. On the right side a vertical lesion breaks through from the dorsal surface and widens out in the central portion to form an area of fine fibers very loosely scattered which merges without definite boundary into the surrounding tissue. The vertical portion of the break is rather clearly defined and bordered on its medial aspect by densely staining material.

It is much to be regretted from the neurological side that more material could not be saved for further study. More sections from the above series might have been drawn; but as only the extent and location of the gross lesions can be determined, because of the condition of the material, such drawings would only multiply cases.

3. Summary

The foregoing evidence presented in the case reports and in the microscopic study of the neurological material available makes it quite clear that definite cerebral lesions were suffered by rats that had undergone the surgical interference. It is felt that the mere fact of cerebral injury to the frontal regions forms a quite sufficient basis for the main purposes of this study and the conclusions to be drawn from it in a later section. This fact has been established. It remains to bring together a few facts that have appeared in isolation in this paper and to correlate them with the findings of previous workers, before we go on to present the experimental results in the mazes themselves.

It is not possible with the material at our disposal to make a very exact estimate of the extent of the cortical lesions. Judging from the position of the openings made in the skull and from the microscopic studies, the knife entered not more than three or four millimeters back of the anterior tip of each hemisphere.

At this point the lesion was superficial, as the knife was inserted at an angle of about forty-five degrees with the horizontal. There can be no question of injury to the basal nuclei; for, while the head of the caudate nucleus is present, it is situated far enough below the surface to be quite out of reach of a knife entering the cortex at such an angle. In fact, the knife would have to be passed in almost vertically to injure the caudate. The lesions in our material would seem to have reached the center of the cerebral structure at a point about 1.2 mm or less from the frontal poles. They would thus average about two-thirds the area estimated by Lashley and Franz (1917) to have been involved in their experiments with the simple two-choice problem. Our experiments involved cortical areas that probably did not exceed in extent that designated by Fortuyn as "area f," in some cases possibly also "area f′" (Craigie, 1925).

Work done upon the question of the electrically stimulable areas of the rat's brain indicate a diffuse type of cortex for this animal, in which movements can be elicited at points scattered over the anterior two-thirds of the dorsolateral aspect of the cortex (Lashley, 1920). These points are not sharply localized, but seem to be surrounded by ill-defined areas which are interpreted by some authors as being to some degree comparable to the so-called "association areas" of the higher mammals. Examination of the case reports in our paper reveals a quite general tendency on the part of the operated rats toward disturbances of both posture and movement. All animals operated upon showed some disturbances of muscular coördination. Eight exhibited distinct disturbances of locomotion, in some cases both fore and hind limbs being affected; eight carried the head tilted to one side or the other; five evinced an almost insane tendency to hang over the edge of the observation table, returning repeatedly when removed to the center. The specific disturbances are too numerous separately to be described here. Some of them persisted into the beginning of the maze-running, a period of two weeks or more; most of them were transitory, but their improvement was so very gradual that the disturbances cannot be

laid to surgical shock. This completes the report on the effects of the operations. The next pages are devoted to a presentation of the experimental data gathered in the learning of a series of different maze patterns in accordance with the plan outlined above in Section III, 3.

V. EXPERIMENTAL RESULTS

We are now ready to take up the effects upon the formation, retention, and modification of those habits forced by the mazes shown in figures 2–6, to which the reader is referred for a proper understanding of the following report. A preliminary study of the data gathered revealed the fact that nothing of any value can be derived from the time records; hence, in this report only the errors made during the trials will be considered. The term *error* is taken in this paper to mean the entrance into a cul-de-sac or the retracing of the true path in the wrong direction. In the pages following are given tables representing the average number of errors made in the different groups for each run in each of the mazes (tables 2–5). From these tables have been prepared the learning curves presented in figures 13–24 inclusive. Figures 13–15 give comparisons between the learning curves for groups A and C respectively, in their three tasks before the former group had undergone the cerebral operation. This furnishes a basis for the comparisons made in the three succeeding figures (16–18) between the same groups after the members of group A had been operated upon. In figures 19–21 a comparison is struck between the two groups that differ from the preceding two in that they were given no training before being started in Maze II. Members of group B, it will be remembered, were operated upon two weeks before the beginning of this their very first task; while with group D the operation was omitted but the other conditions kept exactly the same, thus providing a normal control group on B. In figures 22–24 we have a somewhat different situation. These give us, instead of a contrast between an abnormal group and its normal controls, a comparison between the achievements of two groups both of which have been operated upon, *viz.*, groups A and B. In this way the question as to whether or not there has been any retention at all on the part of group A, which had received previous training, has its answer. For

convenience in reference the following little table, listing the four groups and giving their significance in the problems, is appended.

TABLE 1

SIGNIFICANCE OF THE TERMS A, B, C, AND D

Group	Maze patterns in order used	Operation performed
A	I, Ia, II, II (retention), IIa, IIb.	Before II (retention)
B	II, IIa, IIb	Before II
C	I, Ia, II, II (retention), IIa, IIb.	None; normal control on group A
D	II, IIa, IIb	None; normal control on group B

It should be noted that the tables presented in the next pages, and the learning curves derived from them, represent averages for the different groups and not individual records. Tables giving the error records for individual animals are omitted from this paper because of the prohibitive cost of reproduction in print. Since, however, it is sometimes desirable to have access to data from which to study individual variations and their effects upon the records of a group, the writer has deposited copies of these tables together with some others on related material in the library of the University of Michigan. This collection of tables, comprising some seventy-five pages of data, may be obtained for study through any library having exchange privileges with that institution. The title appears in the bibliography at the end of this paper (Cameron, 1927).

The tables of average errors and their derived curves follow, accompanied by an analysis of the curves. The reader is referred to Section III, 3, *Experimental Procedure,* for a statement of the procedure followed in each of the four groups.

TABLE 2

AVERAGE NUMBER OF ERRORS IN GROUP A FOR EACH TRIAL

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
1........	20.9	10.4	21.3	6.4	10.6	14.0
2........	16.3	4.0	19.6	3.4	7.5	6.9
3........	9.3	3.0	16.9	4.5	5.3	2.8
4........	6.0	4.5	16.3	4.4	4.4	1.8
5........	9.5	4.3	12.3	1.8	1.6	0.9
6........	6.8	4.0	5.5	3.0	4.3	1.5
7........	8.0	4.9	5.6	2.5	2.3	1.5
8........	5.3	4.1	5.4	2.8	1.9	2.8
9........	6.1	2.1	4.1	7.0	1.5	0.9
10........	4.5	3.6	6.8	2.6	3.6	2.9

TABLE 2—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
11........	5.0	2.5	8.5	1.4	0.6	1.6
12........	3.1	2.1	4.8	1.6	2.1	1.4
13........	5.0	3.1	5.0	1.0	1.0	1.0
14........	4.5	3.4	4.0	4.6	2.6	0.4
15........	1.6	1.8	3.9	2.3	1.4	2.3
16........	2.9	1.8	3.0	3.1	1.5	0.1
17........	2.0	1.9	4.8	1.0	0.8	0.4
18........	3.8	2.4	1.8	1.3	1.8	0.4
19........	2.5	3.1	2.8	1.0	1.6	0.5
20........	2.1	2.8	1.3	1.8	1.8	0.1
21........	3.0	2.5	4.4	0.8	1.8	0.8
22........	1.3	2.4	2.0	1.5	1.5	0.3
23........	1.1	2.3	2.1	0.8	1.0	0.4
24........	1.0	2.3	1.5	0.8	1.8	0.0
25........	2.4	1.5	1.9	0.4	1.3	0.4
26........	1.3	4.5	2.4	0.5	0.9	0.6
27........	0.3	1.5	3.1	0.6	1.3	0.4
28........	1.3	2.4	1.6	1.0	1.0	0.3
29........	1.1	2.5	3.0	0.4	0.8	1.0
30........	0.4	1.6	3.4	0.8	1.1	0.3
31........	0.6	4.8	0.9	2.6	1.8	0.9
32........	1.5	2.6	1.1	0.5	2.4	0.5
33........	0.8	1.6	2.0	1.5	1.9	0.0
34........	1.4	1.8	2.8	1.9	1.1	1.5
35........	1.0	1.4	2.3	0.8	0.4	0.3
36........	1.0	1.4	0.4	0.8	2.1	0.0
37........	1.3	1.0	0.9	0.6	1.1	0.0
38........	1.4	1.3	0.4	1.1	0.1	0.4
39........	0.8	1.1	0.9	0.8	0.1	0.4
40........	0.8	1.8	1.4	1.3	2.8	0.6
41........	0.5	0.5	2.5	0.3	1.0	0.8
42........	1.1	2.9	0.8	0.1	0.6	0.0
43........	2.6	1.6	2.5	0.8	1.3	0.0
44........	0.9	1.8	1.4	0.8	1.3	0.0
45........	2.8	0.1	1.6	0.4	0.9	0.3
46........	0.4	0.5	0.9	0.3	1.3	0.9
47........	0.1	0.3	2.8	0.3	0.4	0.3
48........	0.5	0.1	3.1	0.8	0.3	0.0
49........	0.8	0.8	2.4	1.3	0.6	0.1
50........	0.1	0.6	0.8	0.3	0.8	0.0
51........	0.4	0.5	1.8	2.5	0.8	0.0
52........	0.3	0.8	0.9	0.6	0.4	0.0
53........	0.3	0.3	1.0	1.0	0.3	0.0
54........	0.3	0.4	1.4	0.6	0.5	0.0
55........	0.1	0.5	1.0	1.4	0.0	
56........	0.9	0.5	0.1	2.3	1.5	
57........	0.1	0.3	0.2	2.3	0.4	
58........	0.5	0.3	0.1	2.0	0.4	
59........	0.1	0.3	0.1	1.0	0.0	
60........	0.4	0.6	0.3	1.1	0.4	

TABLE 2—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
61........	0.1	0.1	0.3	0.8	0.6	
62........	0.3	0.9	0.0	1.4	0.4	
63........	0.6	0.1	0.0	0.5	0.0	
64........	0.4	0.6	0.0	1.5	1.0	
65........	0.3	0.6	0.0	1.1	0.0	
66........	1.1	0.1	0.0	0.4	0.5	
67........	0.3	0.0		1.0	0.1	
68........	0.3	1.1		1.3	1.3	
69........	0.3	0.3		3.5	1.4	
70........	0.0	0.1		0.5	3.1	
71........	0.3	0.5		0.8	0.1	
72........	0.0	0.0		0.5	0.8	
73........	1.1	0.0		1.0	0.0	
74........	0.1	0.0		0.6	0.1	
75........	0.3	0.0		1.4	0.3	
76........	0.3	0.0		0.4	0.8	
77........	0.5			0.3	0.1	
78........	0.9			0.4	1.4	
79........	0.3			1.0	1.1	
80........	0.5			0.6	0.6	
81........	1.3			1.4	2.3	
82........	0.8			0.1	1.4	
83........	4.1			0.5	0.5	
84........	0.3			0.3	0.0	
85........	0.5			0.5	0.3	
86........	0.4			4.5	0.3	
87........	1.1			0.4	0.0	
88........	0.4			0.6	0.1	
89........	0.6			0.8	0.3	
90........	1.5			0.9	0.0	
91........	0.5			0.4	0.5	
92........	0.0			0.5	0.6	
93........	0.1			1.1	0.6	
94........	0.0			0.4	0.4	
95........	0.0			0.6	0.5	
96........	0.0			0.6	0.8	
97........	0.3			0.9	0.1	
98........	0.4			1.1	0.1	
99........	0.3			0.4	0.5	
100........	0.0			1.6	0.3	
101........	0.0			0.0	0.5	
102........	0.3			0.6	0.4	
103........	0.1			1.0	0.1	
104........	0.0			1.0	0.3	
105........	0.1			0.4	0.3	
106........	0.0			0.5	0.3	
107........	0.0			0.8	0.1	
108........	0.0			0.5	0.5	
109........	0.0			0.3	0.4	
110........	0.0			0.3	0.1	

TABLE 2—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
111........				2.3	0.0	
112........				0.3	0.1	
113........				0.8	0.3	
114........				1.5	0.3	
115........				0.3	0.0	
116........				0.1	0.5	
117........				0.3	1.5	
118........				0.5	0.0	
119........				0.4	1.0	
120........				0.1	0.1	
121........				0.6	1.9	
122........				0.3	0.5	
123........				0.4	0.3	
124........				0.4	0.5	
125........				0.3	0.4	
126........				0.1	0.1	
127........				0.8	0.1	
128........				0.8	0.1	
129........				0.5	0.1	
130........				0.3	0.0	
131........				0.5	0.0	
132........				1.0	0.0	
133........				0.1	0.0	
134........				1.0	0.0	
135........				0.1		
136........				0.8		
137........				1.5		
138........				0.8		
139........				0.5		
140........				0.8		
141........				0.1		
142........				0.1		
143........				0.1		
144........				0.1		
145........				0.1		
146........				0.6		
147........				0.0		
148........				0.3		
149........				0.1		
150........				0.0		
151........				0.3		
152........				0.0		
153........				0.8		
154........				0.5		
155........				0.1		
156........				0.0		
157........				0.5		
158........				0.0		
159........				0.1		
160........				0.6		

TABLE 2—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
161				0.1		
162				0.0		
163				0.1		
164				0.0		
165				0.5		
166				0.4		
167				0.4		
168				0.0		
169				0.1		
170				0.1		
171				0.9		
172				0.4		
173				0.5		
174				0.0		
175				0.5		
176				0.0		
177				0.0		
178				0.1		
179				0.0		
180				0.0		
181				0.3		
182				0.0		
183				0.1		
184				0.0		
185				0.3		
186				0.0		
187				0.3		
188				0.0		
189				0.1		
190				0.0		
191				0.6		
192				0.1		
193				0.0		
194				0.0		
195				0.0		
196				0.0		
197				0.1		
198				0.0		
199				0.5		
200				0.0		
201				0.0		
202				0.1		
203				0.4		
204				0.0		
205				0.4		
206				0.0		
207				0.0		
208				0.1		
209				0.4		
210				0.1		

TABLE 2—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
211........				0.0		
212........				0.1		
213........				0.0		
214........				0.4		
215........				0.3		
216........				0.0		
217........				0.1		
218........				0.0		
219........				0.8		
220........				1.1		
221........				0.0		
222........				0.0		
223........				0.1		
224........				0.0		
225........				0.1		
226........				0.1		
227........				0.0		
228........				0.0		
229........				0.0		
230........				0.0		
231........				0.0		

TABLE 3

AVERAGE NUMBER OF ERRORS IN GROUP B FOR EACH TRIAL

Trial	Maze II	IIa	IIb
1..................	26.7	13.5	26.8
2..................	38.3	5.5	6.5
3..................	32.4	4.8	3.3
4..................	24.8	4.0	4.8
5..................	16.3	3.8	2.2
6..................	15.5	5.7	0.8
7..................	12.8	2.8	0.2
8..................	10.5	5.8	0.2
9..................	20.6	3.0	0.8
10..................	7.0	1.8	0.8
11..................	6.1	2.0	0.5
12..................	6.8	2.5	1.0
13..................	4.5	2.0	0.5
14..................	7.0	4.2	0.2
15..................	3.1	1.3	0.5
16..................	5.5	2.8	0.3
17..................	2.8	2.2	0.3
18..................	3.8	2.7	0.3
19..................	3.0	3.3	0.7
20..................	3.3	1.8	0.5
21..................	2.5	1.5	0.8
22..................	5.5	5.7	0.0
23..................	1.6	2.2	0.2
24..................	3.8	1.5	0.3
25..................	3.0	3.7	2.5

TABLE 3—*Continued*

Trial	Maze II	IIa	IIb
26	3.3	1.5	0.8
27	7.0	5.7	1.5
28	4.3	3.5	0.3
29	0.8	1.3	0.5
30	4.3	1.0	0.0
31	4.3	2.5	1.2
32	1.3	2.5	0.3
33	4.8	2.7	0.5
34	1.2	2.0	0.0
35	2.2	1.3	0.2
36	2.8	2.0	0.0
37	1.7	1.5	0.2
38	2.8	0.5	0.0
39	3.0	2.5	0.3
40	2.5	0.8	0.0
41	1.2	0.5	0.2
42	1.3	0.8	0.2
43	1.2	1.0	0.2
44	2.0	1.8	0.0
45	2.3	0.7	0.0
46	0.8	0.2	0.0
47	0.7	0.5	0.0
48	1.8	1.0	0.0
49	1.5	0.5	
50	1.3	0.3	
51	4.5	0.3	
52	1.7	1.7	
53	0.5	0.7	
54	0.7	1.3	
55	1.2	0.8	
56	5.5	0.8	
57	1.5	0.5	
58	2.2	0.3	
59	1.0	0.5	
60	3.2	0.0	
61	1.3	0.3	
62	0.5	0.0	
63	3.2	0.3	
64	3.3	0.0	
65	0.7	0.8	
66	1.3	0.2	
67	0.5	0.7	
68	1.0	0.0	
69	2.2	0.0	
70	1.7	0.2	
71	0.5	0.3	
72	1.3	0.2	
73	1.3	0.2	
74	0.3	0.2	
75	1.3	0.7	

TABLE 3—*Continued*

Trial	Maze II	IIa	IIb
76	4.2	0.0	
77	0.7	0.3	
78	0.3	0.5	
79	0.0	0.3	
80	0.2	0.0	
81	1.8	0.5	
82	9.2	0.2	
83	3.8	0.5	
84	1.0	0.8	
85	9.5	0.5	
86	3.2	1.2	
87	1.0	0.7	
88	1.0	1.2	
89	0.3	0.2	
90	0.5	0.3	
91	0.3	0.3	
92	0.7	0.2	
93	0.5	0.0	
94	0.5	0.0	
95	0.2	0.2	
96	0.7	0.0	
97	0.8	0.3	
98	0.3	0.2	
99	0.2	0.2	
100	0.3	0.0	
101	0.2	0.0	
102	0.5	0.2	
103	0.8	0.2	
104	0.0	0.2	
105	0.7	0.0	
106	1.7	0.2	
107	0.5	0.0	
108	0.7	0.0	
109	0.3	0.3	
110	0.0	0.0	
111	0.0	0.2	
112	0.7	0.0	
113	0.2	0.0	
114	0.7	0.0	
115	1.5	0.0	
116	0.3	0.2	
117	0.3	0.0	
118	0.2	0.0	
119	0.7	0.0	
120	0.8	0.0	
121	1.0	0.3	
122	0.2	0.2	
123	1.5	0.3	
124	0.3	0.0	
125	0.3	0.2	

TABLE 3—*Continued*

Trial	Maze II	IIa	IIb
126	1.3	0.0	
127	0.5	0.2	
128	0.2	0.0	
129	0.5	0.2	
130	0.0	0.0	
131	4.3	0.0	
132	0.2	0.2	
133	0.0	0.0	
134	0.0	0.0	
135	0.5	0.0	
136	0.2	0.0	
137	1.0	0.0	
138	2.5		
139	1.3		
140	0.0		
141	0.8		
142	0.0		
143	0.3		
144	0.2		
145	1.8		
146	0.0		
147	0.5		
148	0.5		
149	0.0		
150	0.2		
151	0.3		
152	0.0		
153	0.3		
154	0.2		
155	0.0		
156	0.0		
157	0.0		
158	0.0		
159	0.3		
160	0.0		
161	0.3		
162	0.0		
163	0.0		
164	0.5		
165	0.0		
166	0.2		
167	0.0		
168	0.0		
169	0.0		
170	0.0		
171	0.0		

TABLE 4

AVERAGE NUMBER OF ERRORS IN GROUP C FOR EACH TRIAL

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
1........	34.0	10.2	48.2	8.1	12.3	20.4
2........	24.4	4.6	31.7	4.8	7.0	12.2
3........	16.8	4.6	33.3	4.5	6.9	4.7
4........	13.5	2.2	21.3	2.8	6.4	3.2
5........	9.3	2.2	18.9	2.1	3.4	3.9
6........	9.4	3.3	13.5	3.0	3.8	0.9
7........	8.7	1.8	12.4	3.9	2.5	1.5
8........	7.5	1.6	7.4	1.2	2.0	0.9
9........	7.2	1.5	7.3	2.1	2.5	0.7
10........	5.4	2.9	6.9	2.1	2.4	0.2
11........	5.4	2.0	7.4	1.9	2.2	0.2
12........	5.8	1.5	5.8	4.8	2.8	0.1
13........	7.3	1.1	3.9	1.8	1.6	0.2
14........	4.7	0.6	3.5	0.7	1.8	0.0
15........	5.1	1.4	2.7	2.4	1.5	0.5
16........	3.9	0.8	2.5	1.5	2.5	0.0
17........	3.5	0.8	3.2	1.1	1.9	0.2
18........	3.8	0.4	3.7	1.7	1.1	0.1
19........	3.8	0.6	1.9	1.3	0.9	0.0
20........	3.6	0.3	1.5	1.4	1.3	0.1
21........	3.5	0.9	2.4	2.0	0.7	0.0
22........	2.9	0.5	2.1	0.7	2.1	0.0
23........	2.7	0.5	2.5	0.5	1.4	0.0
24........	3.7	0.7	1.8	0.9	0.5	0.0
25........	2.7	0.3	1.2	0.8	0.7	0.2
26........	2.9	0.3	1.2	1.0	0.5	0.0
27........	1.8	0.7	2.1	1.2	0.4	0.1
28........	3.2	1.5	1.9	0.1	0.5	0.0
29........	3.1	0.5	2.4	0.5	0.4	0.1
30........	2.7	0.4	1.8	0.4	0.6	0.0
31........	2.0	0.2	0.8	0.5	0.4	0.1
32........	2.0	0.0	1.5	0.2	0.2	0.0
33........	2.4	0.4	1.2	0.5	0.2	0.0
34........	1.5	0.4	1.7	0.3	0.7	0.0
35........	3.9	0.1	1.9	0.0	0.4	0.0
36........	3.0	0.4	1.8	0.3	0.3	0.0
37........	1.8	0.0	1.4	0.2	0.2	
38........	1.4	0.2	1.3	0.1	0.1	
39........	1.7	0.1	1.0	0.1	0.1	
40........	2.4	0.0	1.4	0.8	0.1	
41........	1.4	0.1	1.2	0.5	0.2	
42........	3.4	0.1	0.9	0.3	0.2	
43........	2.3	0.0	0.9	0.1	0.2	
44........	1.8	0.1	1.1	0.2	0.1	
45........	0.9	0.2	0.7	0.4	0.5	

TABLE 4—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
46........	1.4	0.0	1.5	1.7	0.5	
47........	0.8	0.0	0.8	0.1	0.1	
48........	2.1	0.1	1.1	0.0	0.2	
49........	1.1	0.2	0.7	0.1	0.1	
50........	1.1	0.1	0.8	0.1	0.1	
51........	1.3	0.0	0.5	0.3	0.1	
52........	0.8	0.0	0.4	0.1	0.1	
53........	0.9	0.0	0.9	0.2	0.1	
54........	1.0	0.0	0.8	0.1	0.1	
55........	0.8	0.0	0.7	0.1	0.2	
56........	0.7		0.7	0.0	0.1	
57........	0.9		0.3	0.1	0.1	
58........	0.5		0.4	0.1	0.1	
59........	1.1		0.3	0.0	0.1	
60........	1.8		0.3	0.0	0.1	
61........	0.8		0.5	0.0	0.1	
62........	1.0		0.4	0.0	0.1	
63........	0.4		0.4	0.0	0.1	
64........	0.7		0.7		0.1	
65........	0.6		0.5		0.1	
66........	1.1		0.2		0.1	
67........	0.8		0.3		0.1	
68........	0.7		0.1		0.1	
69........	1.4		0.1		0.2	
70........	0.7		0.2		0.1	
71........	0.5		0.2		0.1	
72........	0.6		0.4		0.1	
73........	0.6		0.4		0.0	
74........	1.1		0.8		0.0	
75........	0.2		0.1		0.0	
76........	1.1		0.1		0.0	
77........	0.3		0.4		0.0	
78........	0.8		0.2			
79........	0.4		0.2			
80........	0.3		0.2			
81........	0.3		0.4			
82........	0.4		0.1			
83........	0.2		0.1			
84........	0.6		0.1			
85........	0.6		0.0			
86........	0.4		0.0			
87........	0.6		0.0			
88........	0.5		0.0			
89........	0.2		0.0			
90........	0.2					
91........	0.2					
92........	0.1					
93........	0.2					
94........	0.1					
95........	0.3					

TABLE 4—*Continued*

Trial	Maze I	Ia	II pre-ret.	II post-ret.	IIa	IIb
96	0.2					
97	0.2					
98	0.1					
99	0.2					
100	0.3					
101	0.2					
102	0.4					
103	0.1					
104	0.1					
105	0.1					
106	0.1					
107	0.1					
108	0.0					
109	0.0					
110	0.0					
111	0.0					
112	0.1					
113	0.0					
114	0.0					
115	0.1					
116	0.1					
117	0.1					
118	0.1					
119	0.1					
120	0.1					
121	0.0					
122	0.2					
123	0.1					
124	0.0					
125	0.0					
126	0.0					
127	0.1					
128	0.1					
129	0.1					
130	0.2					
131	0.1					
132	0.2					
133	0.0					
134	0.0					
135	0.0					
136	0.0					
137	0.0					

TABLE 5

AVERAGE NUMBER OF ERRORS IN GROUP D FOR EACH TRIAL

Trial	Maze II	IIa	IIb
1	29.2	15.8	27.0
2	27.6	10.0	7.2
3	23.6	10.0	4.8
4	14.2	4.8	3.8
5	17.8	3.2	4.0
6	9.4	3.4	2.8
7	7.0	3.0	0.4
8	8.4	3.0	1.0
9	9.0	1.8	0.2
10	4.6	2.6	0.8
11	4.4	2.4	0.2
12	5.2	2.4	0.4
13	4.4	2.2	0.2
14	3.0	2.2	0.8
15	5.0	1.2	0.4
16	4.4	2.0	0.0
17	2.8	4.4	0.4
18	3.0	2.0	0.4
19	3.8	2.6	0.0
20	3.4	1.6	0.0
21	5.0	1.4	0.0
22	3.4	5.8	0.0
23	3.2	1.2	0.0
24	2.6	1.4	
25	1.8	0.8	
26	2.6	0.6	
27	4.2	0.2	
28	3.2	1.0	
29	2.2	0.6	
30	1.2	0.8	
31	1.2	1.2	
32	1.4	1.2	
33	2.6	0.4	
34	3.8	0.2	
35	0.8	0.0	
36	0.6	0.2	
37	0.8	0.0	
38	1.4	0.0	
39	0.8	0.4	
40	1.4	0.2	
41	0.4	0.0	
42	0.6	0.0	
43	0.2	0.0	
44	0.2	0.0	
45	0.0	0.0	

TABLE 5—*Continued*

Trial	Maze II	IIa	IIb
46	0.0		
47	0.0		
48	0.4		
49	0.0		
50	0.0		
51	0.0		
52	0.0		
53	0.0		

1. Comparison of Curves for Groups A and C.

A comparison struck between the curves of achievement before the retention period, during which group A was operated upon, fails to show any consistent difference in the records of these two groups, if we except the relatively unimportant fact of greater general irregularity in the performance of group A. Inspection of figures 13–15 brings out the following relations. In Maze I the control group, C, required a greater number of trials for learning than did the group that was later to be operated upon, A; while for Maze Ia the opposite relation holds. If, now, we consider initial performance, group C is again at a disadvantage in Maze I, only one trial in the first thirty showing a better record than the corresponding one in group A and only one other showing as good a record. This is partly compensated for in the greater uniformity of the latter part of the curve for group C in this maze. In Maze Ia, on the other hand, group C has the better of it in the initial as well as in the later trials. Thus we find a greater number of trials required by the control group than by group A for learning Maze I, and a greater number required by A than by C for the learning of Maze Ia; while in the matter of initial trials, A comes off better in the first maze and C in the second. Inspection of figure 15, giving the comparison of the learning curves for Maze II before the operations, reveals the same tendency to irregularity in the curve for group A; but this is certainly compensated for in the very poor early record of C coupled with the fact that C required 35% more trials to learn the maze than A. It would be difficult in studying the records for the preceding three maze patterns to come to any

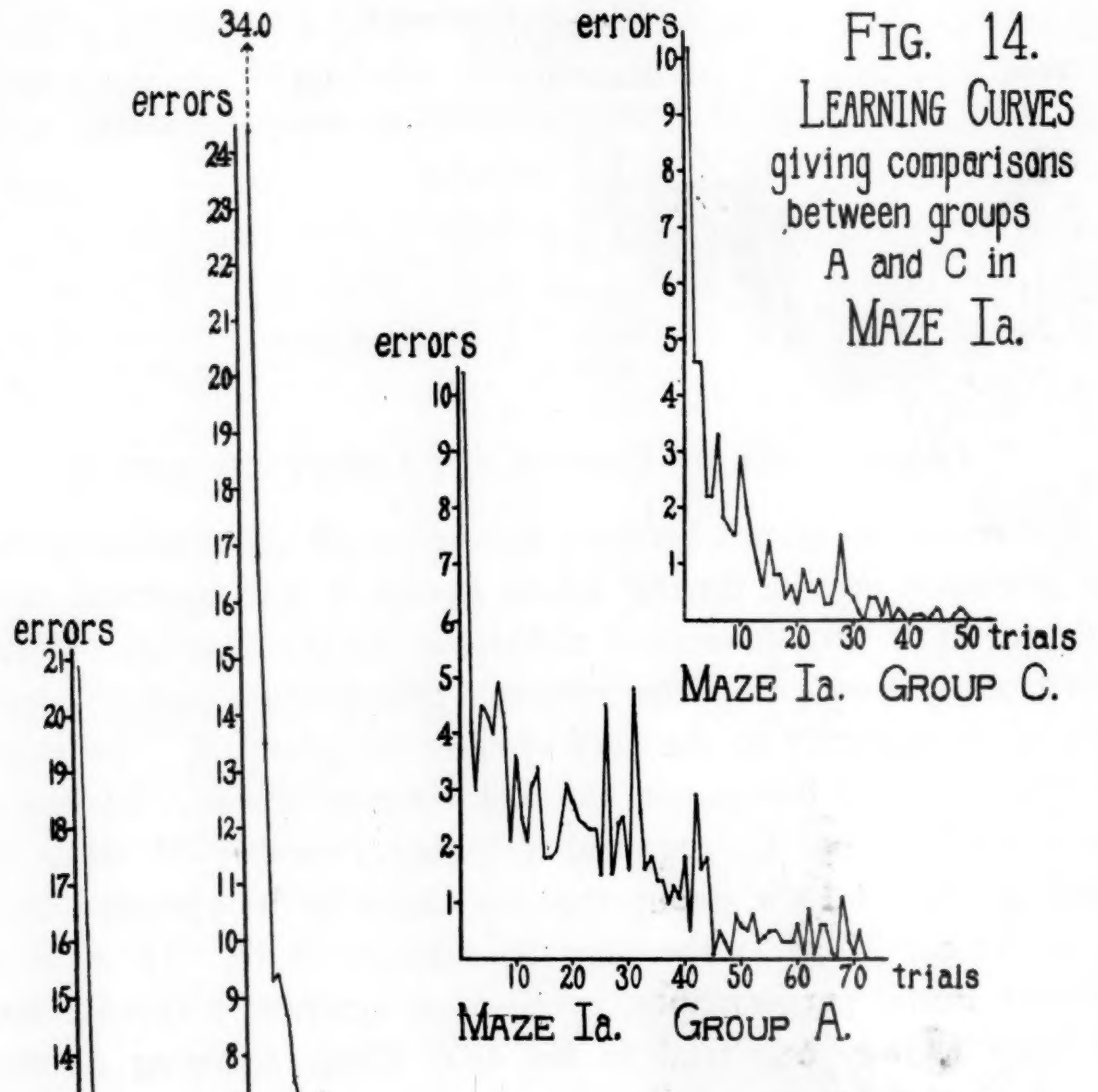


FIG. 14.
LEARNING CURVES
giving comparisons
between groups
A and C in
MAZE Ia.

FIG. 13.
LEARNING CURVES
giving comparisons between
groups A and C in
MAZE I.

very definite decision as to the relative merits of the two groups. We shall find this lack of a consistent relationship in sharp contrast to the consistency that obtains after the operations have been performed.

When we turn to the post-operative curves (figs. 16–18), a rather remarkable relationship appears. The curves in figure 16 give a graphic picture of this. There is a marked coincidence between the anterior parts of the two curves, and an equally

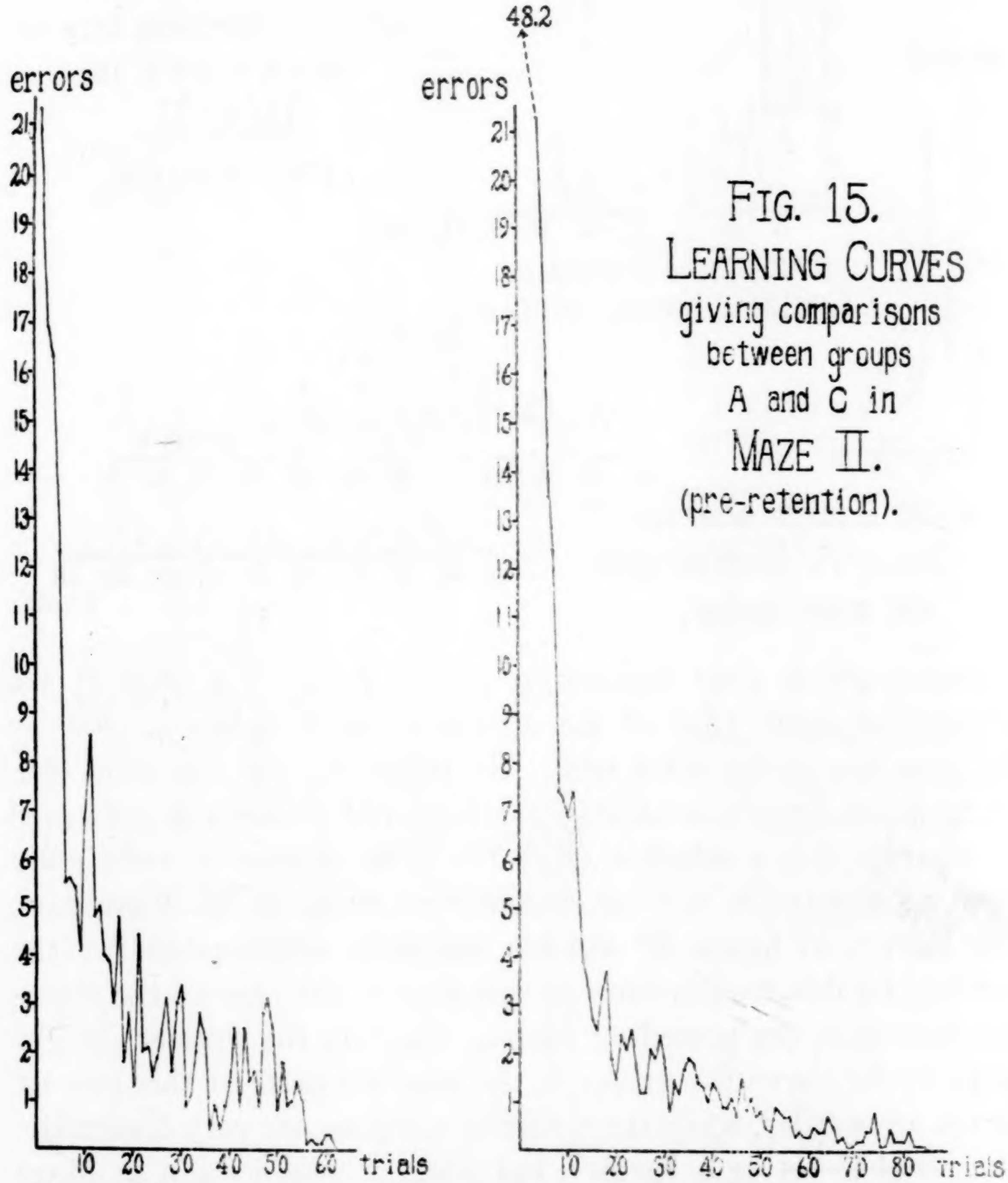


FIG. 15.
LEARNING CURVES
giving comparisons
between groups
A and C in
MAZE II.
(pre-retention).

MAZE II (pre-retention). GROUP A. MAZE II (pre-retention). GROUP C.

marked lack of it in the posterior parts of the same curves. In the figure they have been arbitrarily divided at the same trial in order the better to bring this out. Records of the first few trials are strictly comparable; in fact, the averages for the first twenty-eight trials of the two groups are: A, 2.3 errors, and C, 2.2 errors. But after these first trials the curve for the

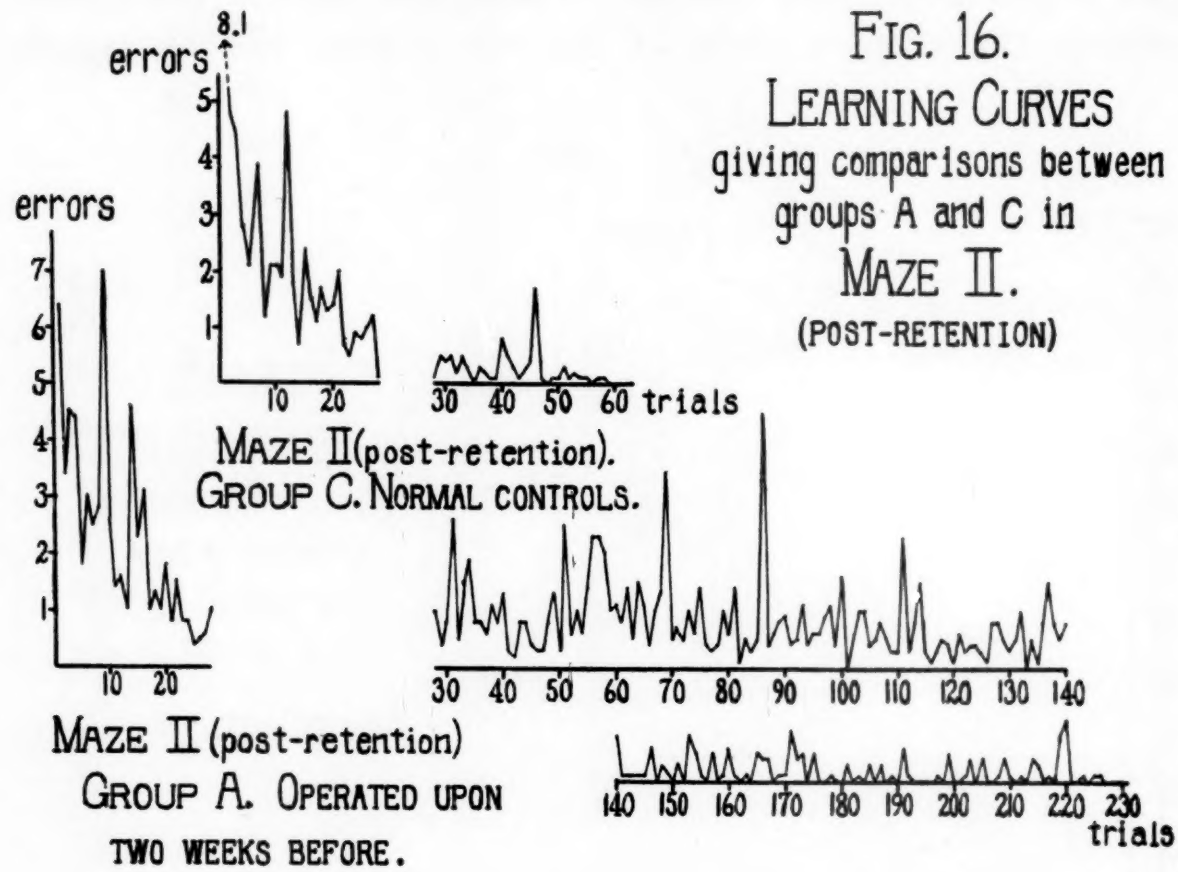
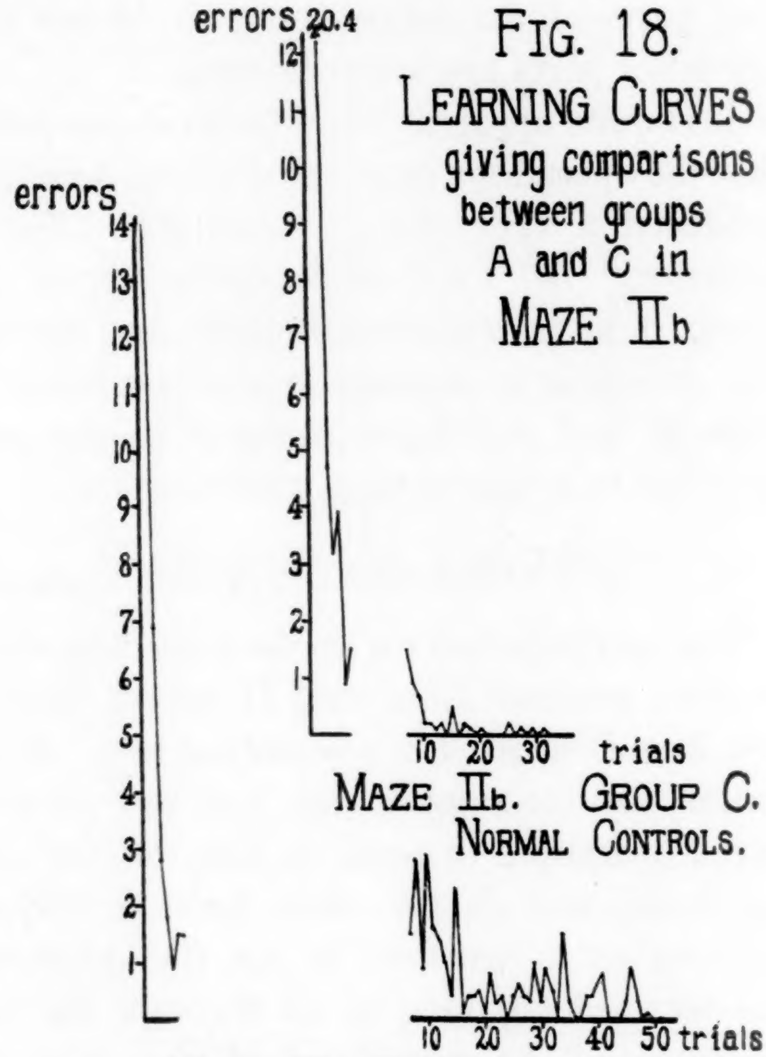


FIG. 16.
LEARNING CURVES
giving comparisons between groups A and C in
MAZE II.
(POST-RETENTION)

operated group goes wandering on, to come to a stop at the 231st trial, while that of the normal controls comes to rest on the base line at the 63rd trial. So much for the retention test. In the next series a modification of the old problem is presented to the rats for a solution (fig. 5). The change is sufficiently great to demand a not inconsiderable adaptation on their part. The curves in figure 17 exhibit the same relationship for the learning of this modification as was seen in the case of the retention curves in the preceding figure. Barring the greater irregularity of the curve for group A, the anterior parts of this pair of curves are similar, while the posterior portions are very dissimilar. The problem set by a further, but slighter modification in Maze IIb (fig. 6) brings out the same sort of comparison again. The

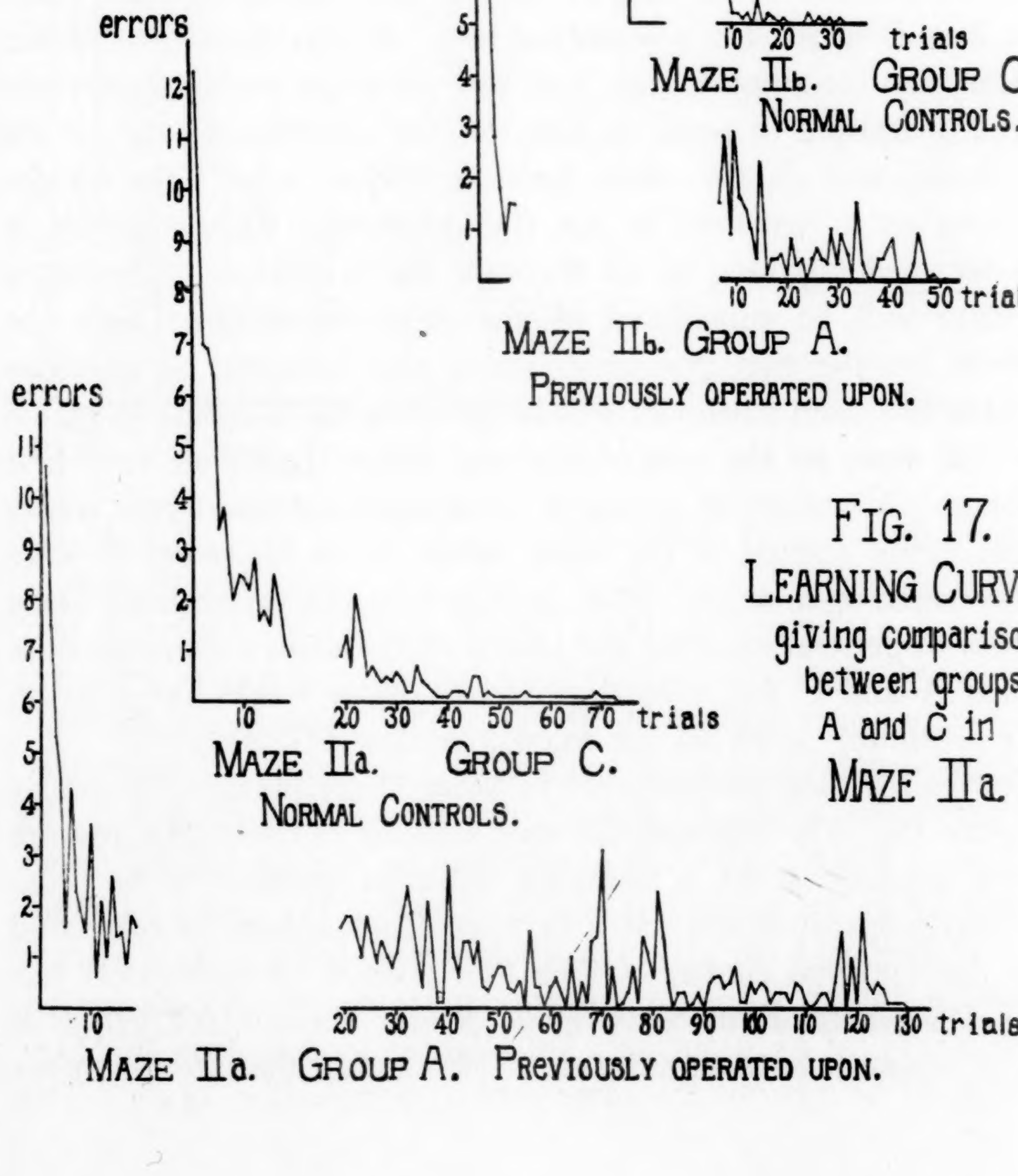
FIG. 18.
LEARNING CURVES
giving comparisons
between groups
A and C in
MAZE IIb



MAZE IIb. GROUP C.
NORMAL CONTROLS.

MAZE IIb. GROUP A.
PREVIOUSLY OPERATED UPON.

FIG. 17.
LEARNING CURVES
giving comparisons
between groups
A and C in
MAZE IIa.



MAZE IIa. GROUP C.
NORMAL CONTROLS.

MAZE IIa. GROUP A. PREVIOUSLY OPERATED UPON.

first parts of the curves in figure 18 are very much alike, while the latter parts are very different.

It is quite apparent from the evidence presented by these curves that the operations upon the cerebral hemispheres of the rats have produced a very clearly discernible effect upon their learning behavior. All the post-operative curves place the learning of group A in an unfavorable light, and the difference between the two groups is as marked as it is consistent. Discussion of these findings and of those reported in the ensuing paragraphs is deferred to a later section (Section VI).

2. Comparison Between Groups B and D.

The rats reported on in the preceding section had been trained in maze patterns I, Ia, and II before their subsequent introduction into II again for a retention test. It was desired to obtain results also on animals that had had no maze training previous to the operation, in order to rule out the retention factor on the one hand, and on the other hand to throw some light on the question as to whether or not the previously trained group A had retained anything at all through the operation. The latter question will be considered in the next sub-section; here the records for the two groups in which the influence of previous training has been ruled out will be compared. The rats in group B and D were set the task of learning Maze II as their very first problem. Members of group B were operated upon two weeks before being started in the maze, while those of group D were not operated upon at all. Both groups were put through the same process of general exercise and placed on the same rations as were groups A and C for a total period of three weeks previous to their beginning work on the maze (Section III, 3).

Curves for their performance in Maze II are presented together in figure 19. The difference is very striking. Their first attempt at the acquisition of a complex behavior pattern finds those previously operated upon at a distinct disadvantage as compared with their normal controls. The first portion of each curve has the same general character. (The poorer showing of group B may or may not have significance. Although it fits into our other

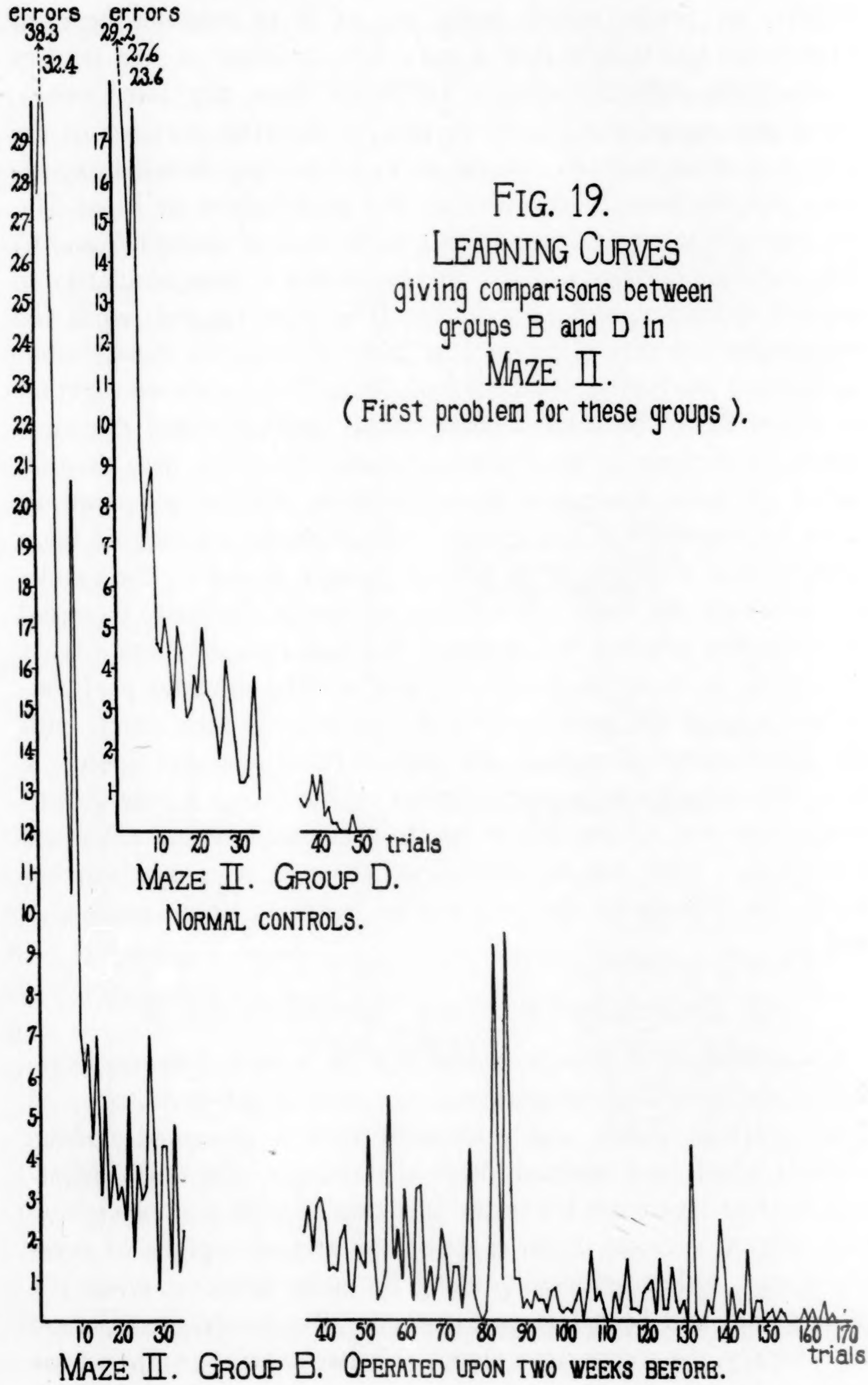


FIG. 19.
LEARNING CURVES
giving comparisons between
groups B and D in
MAZE II.
(First problem for these groups).

results, we prefer not to make use of it as evidence here, as experience has taught that a rat's first problem in life is very much more liable to chance variations than any later ones). After this early resemblance we find, in the after portions of the curves, a divergence so obvious as to render any detailed exposition superfluous. In considering the modification in Maze IIa, we meet the same situation as that in the case of groups A and C. The anterior divisions of the curves exhibit a close similarity in general character, although that of B is more ragged; while the remainders are very different (fig. 20). Curves for these groups in learning the further modification, Maze IIb, are shown together in figure 21. The same relative initial similarity and the same relative difference in later trials appears. We have here another series of three successive maze problems following operations upon the members of one group. Although the training of these animals was different from that of groups A and C, the results are relatively the same. We find a consistent similarity in initial performance whether we compare the post-operative records of A with C, or those of B with D; and we find the later performances showing the same sort of dissimilarity in both pairs, with the disadvantage always on the side of those operated upon. It now only remains to be seen whether or not group A was able to carry over any of the effects of its previous learning after the operations. This can be determined through a comparison between the records of the two groups operated upon, groups A and B.

3. Comparison Between Groups A and B.

Consideration of groups A and B is on a basis different from that of the preceding comparisons. In each of sub-sections 1 and 2 an operated group was contrasted with a group of normal controls which had received identical training. The only difference in their treatment lay in the fact that of each pair one group had suffered surgical disturbance of the frontal regions of cerebral cortex, either before or during the maze learning, while the other group had been left undisturbed. But in this section, on the contrary, the comparison struck is between two groups whose training had been quite different, but whose members had all

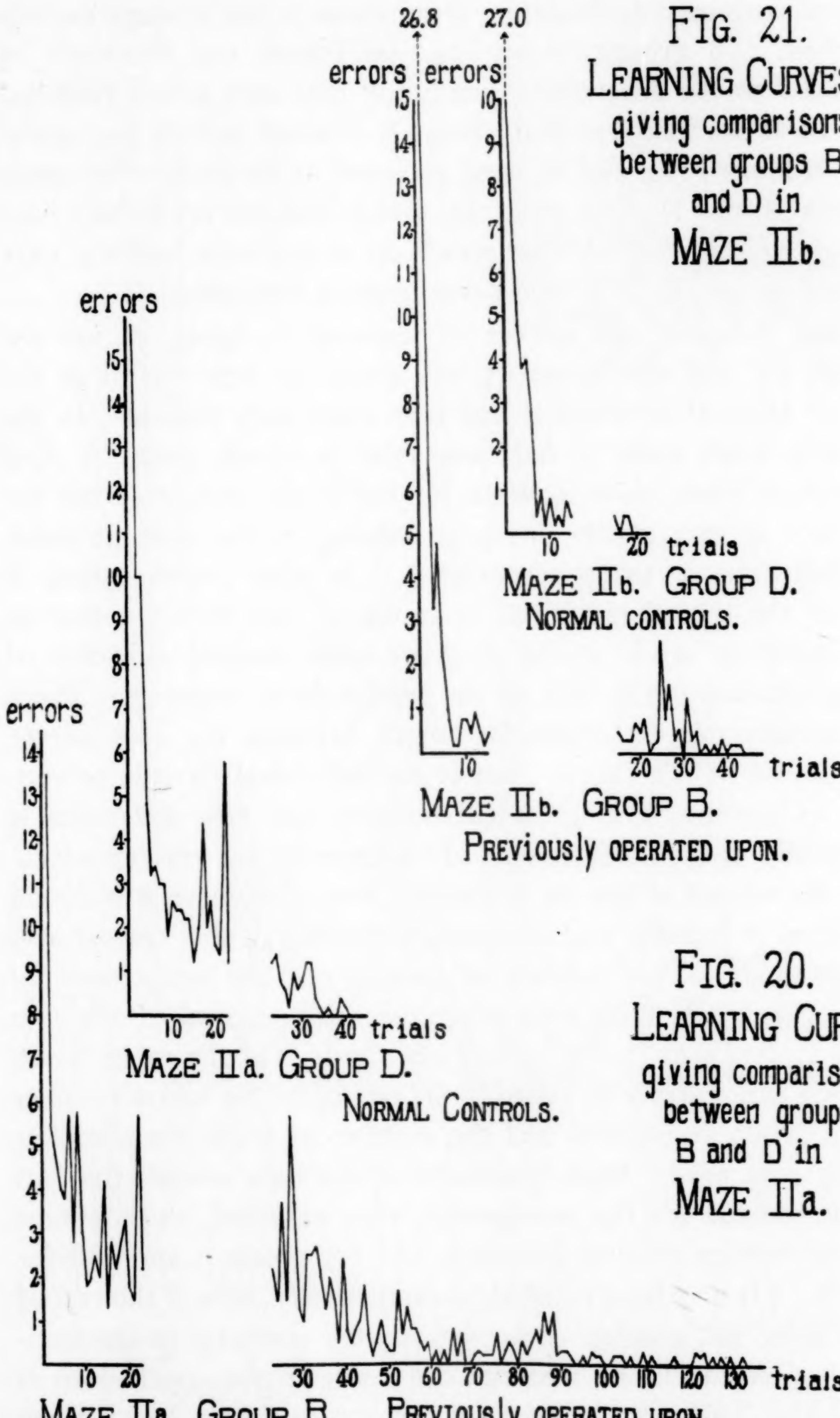


FIG. 21.
LEARNING CURVES
giving comparisons
between groups B
and D in
MAZE IIb.

FIG. 20.
LEARNING CURVES
giving comparisons
between groups
B and D in
MAZE IIa.

suffered surgical interference. Differences in the average records for these two groups, if any can be found, can therefore be attributed to the differences in training that each group received. That is, if we discover that group A, trained before the operations in Maze I, Ia, and II, does no better at the start when again introduced into II than group B, which had not previously been trained, we can conclude that no effects of previous training were retained by group A through the cerebral operation.

When, however, the curves of learning in figure 22 are examined, we find that group A has much the better of it at the start of Maze II in which it had been previously trained. In the first fifty trials there is only one trial in which group A does not make a better showing than B; and in the first ten trials the difference is very great, group B making on the average more than five times as many errors as A. In other words, group B presents the typical picture of a group of rats that are new to maze learning, while group A gives quite definite evidence of having retained not a little of its pre-operative training. There is a considerable difference in length between the two curves which is not in A's favor. But if the individual records be consulted (Cameron, 1927), it will be seen that this difference is due entirely to the performance of one animal, rat number seven. When the record of this rat is omitted from the curve it is found that group A actually makes a better showing in this respect also than group B. This method of leaving out the worst member of one group and then comparing the achievements of the two groups is, however, hardly above criticism. On the other hand, exception can scarcely be taken if the record of the worst member of each group be omitted and the number of trials for complete learning compared. Such treatment of the data reveals the fact that the records for the two groups, thus modified, show almost the same number of trials for each, 151 for group A and 146 for group B. (It may be remarked, parenthetically, that if the record of this same rat, number seven, be omitted similarly in the comparison of A and C, no material difference in the conclusions is arrived at. This may be seen by turning to figure 16.) Even disregarding number of trials for the moment, the difference between the two curves is plainly indicative of retention of the

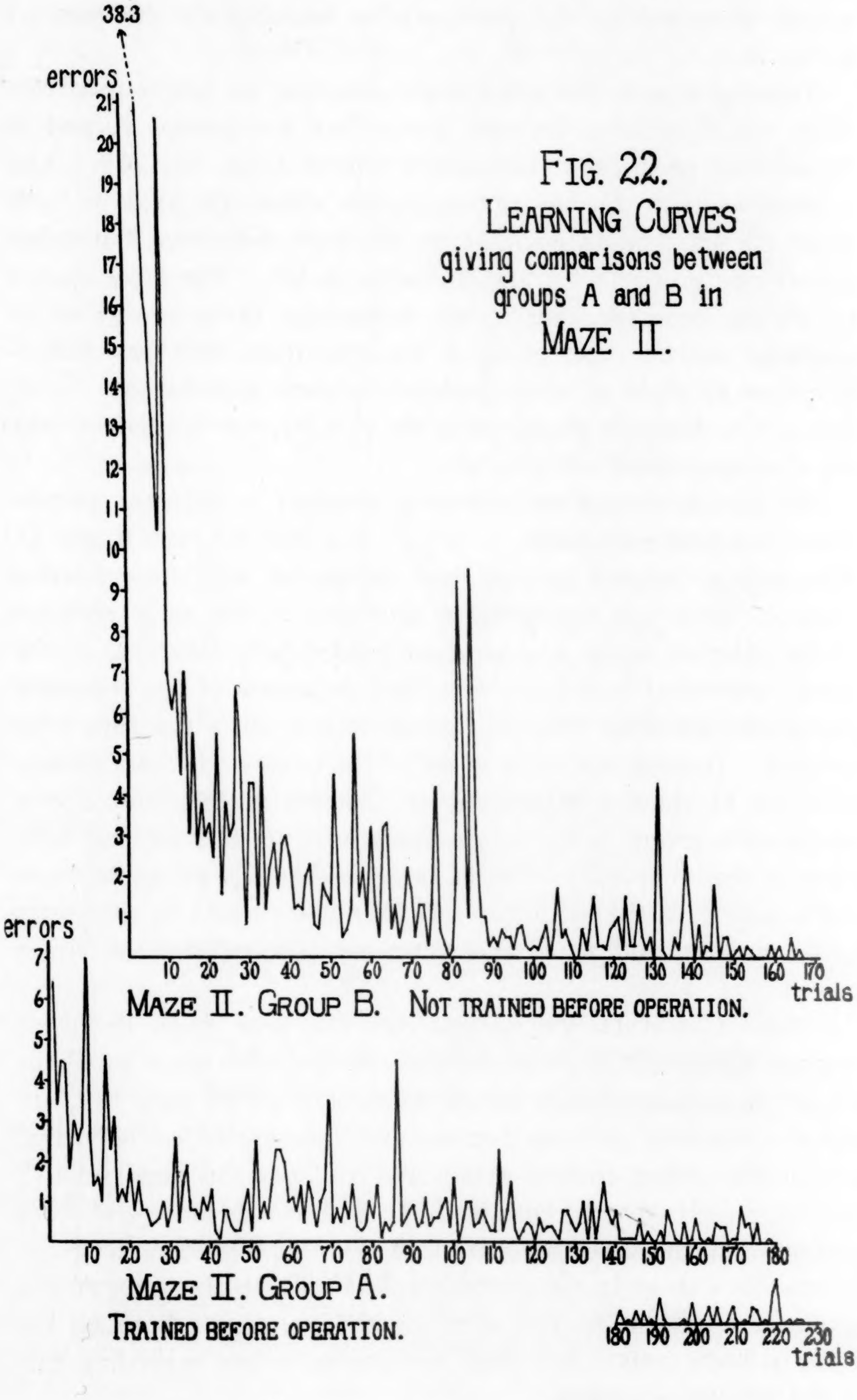


FIG. 22.
LEARNING CURVES
giving comparisons between
groups A and B in
MAZE II.

MAZE II. GROUP B. NOT TRAINED BEFORE OPERATION.

MAZE II. GROUP A.
TRAINED BEFORE OPERATION.

effects produced by the pre-operative learning on the part of group A.

Turning now to the other maze patterns, we find a relatively close correspondence between the curves for groups A and B throughout practically their entire extent (figs. 23, 24). The number of trials for the two groups is almost the same in both Maze IIa and Maze IIb; and even the slight difference that exists favors one group in IIa and the other in IIb. The error record shows the same phenomena; the differences favor one group in one maze and the other group in the other maze, and these differences are so slight as to be probably without significance. Since they are in different directions in the two maze problems, we may say that they cancel one another.

The above comparison certainly presents a different picture from that between groups A and C, and that between B and D. Where the operated groups were compared with their normal controls, there was a consistent similarity in the early portions of the pairs of curves and an equally consistent difference in the latter portions of each pair. But the comparison of one abnormal group with the other abnormal group fails to show the same relationship. Instead, the early parts of the curves for these groups in Maze II show a difference, attributable to retention effects produced in group A by the pre-operative training; and the later parts of these curves, instead of being widely dissimilar, are very much alike. In the modifications, Mazes IIa and IIb, this similarity may be said to extend practically throughout the entire curves.

Groups C and D, the normal controls, bear much the same relation to each other in the three post-operative maze problems as did A and B. Their curves in figures 16–21 may be compared. We may go even further and compare either abnormal group with either control group and still get the same relative results in their curves (figs. 16–21). It becomes more and more evident that the cerebral operations have produced a very unmistakable change in the learning behavior of both group A and group B; futhermore, the effect of the operations is much the same in both cases. We shall have more to say regarding this in the following section.

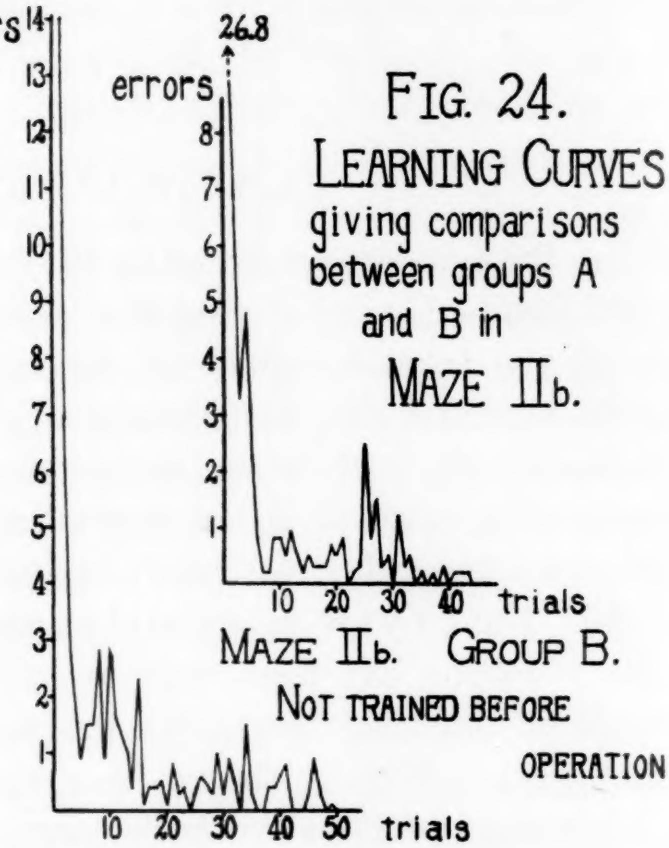


FIG. 24.
LEARNING CURVES
giving comparisons between groups A and B in
MAZE IIb.

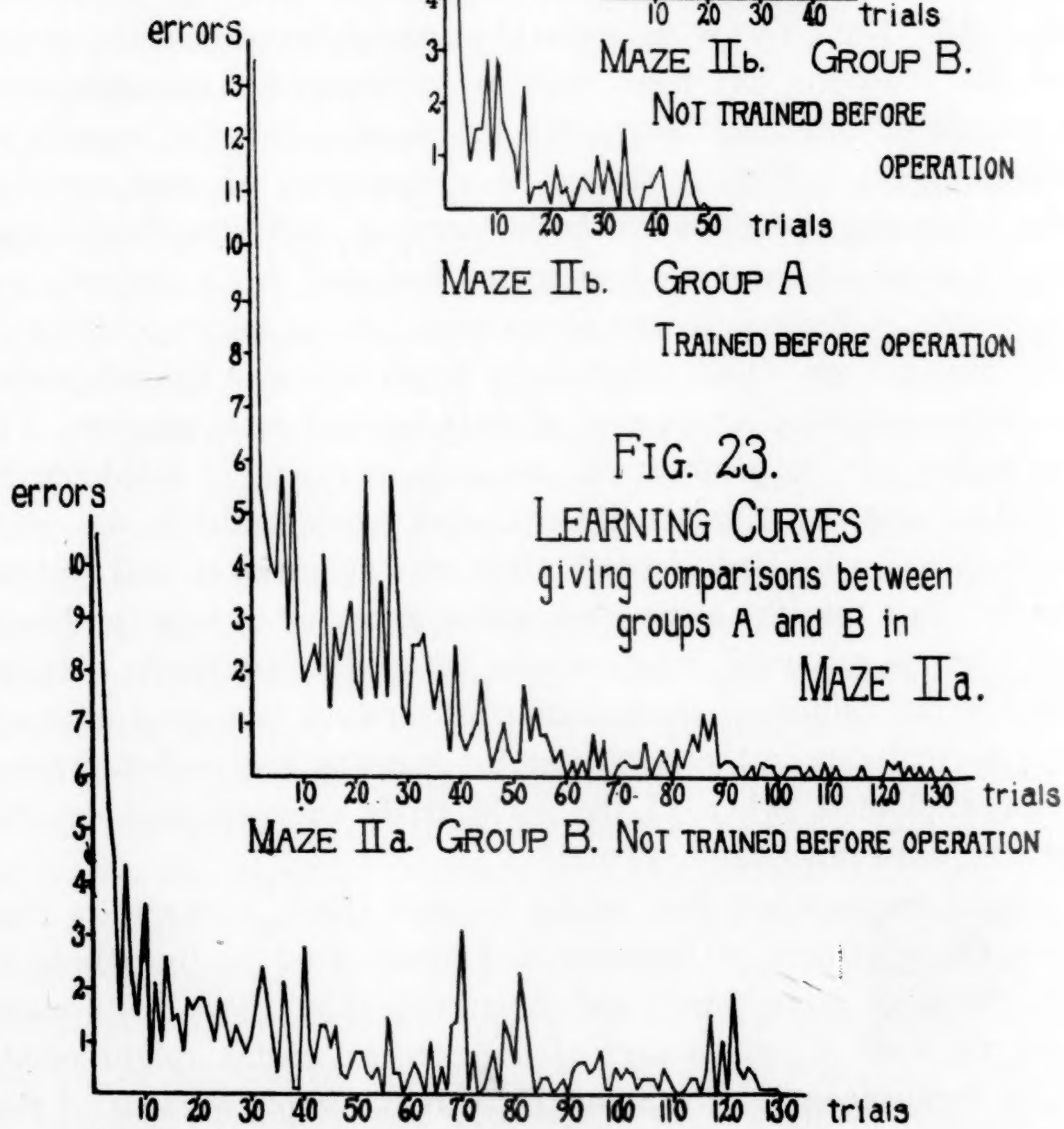


FIG. 23.
LEARNING CURVES
giving comparisons between groups A and B in
MAZE IIa.

VI. CONCLUSIONS.

From the evidence presented by the experiments reported above, we feel justified in concluding that destruction of even small portions of the frontal regions of the rat's cerebral cortex results in quite unmistakable disturbances in the learning and retention of a maze habit, and in adaptations to changes in maze patterns. These results stand in direct contradiction, so far as the experiments are comparable, to those obtained by previous workers in the field. Not only are the general results different, but the setting of the problems has been such as to bring out an unexpected relationship that has heretofore not appeared in the reports on similar work. This is shown in a similarity of appearance in the beginning portions of both learning and retention curves for normal and operated animals, followed by a decided and consistent difference in the appearance of the latter portions of the same curves. This relationship holds true also for adaptation to subsequent modifications of already-learned maze patterns. The possibility of "surgical shock" as an explanation is ruled out by the fact that the animals did not start work again in the maze until two weeks had elapsed after the operations, and by the further fact that the same phenomena appeared in later problems not even begun until many weeks after the operations. How, then, is the failure of those suffering cerebral injury to improve at a normal rate in the latter part of learning and redintegration to be explained, when in the early trials of each problem the records were practically normal?

One interpretation that might suggest itself, perhaps, is that since the responses of decerebrate animals tend on the whole to become more stereotyped and invariable than those of normal ones, the loss of only a part of the cerebral cortex might result in the persistence of certain specific errors, simply because of the lack of some specific cortical components essential to the necessary adaptive changes. But inspection of the detailed records of the

trials of individual animals shows at once that such an interpretation would not fit the experimental results obtained. Failure on the part of the abnormals to meet adequately the problems presented to them in a manner comparable to the record of the normal animals is found not to be due to the presence of some one or two persistent errors, but rather to involve a quite normal distribution of errors. For example, we find rat number four in the last few trials in Maze II after the operation making the following errors: In one trial it enters alleys 6, 16, 14, and 18; in the next trial, alley 4 only; in the next, alley 6; then 16; in the following trial, alleys 2, 4, and 8; in the next 4, 6, and 8; then 8, 10, 12, 14; then alley 2; in the next trial, alley 22; then 4; then alleys 2 and 8; and in the last trial before learning was completed, it enters 12.

The animals seem after the operations to have been unable to meet the problems as a whole as adequately as the normal controls; that is, the operated rats were not able to learn a new problem as a whole so rapidly, and they were unable to redintegrate so readily old problems learned before the surgical interference. Moreover, this state of affairs persisted through the running of one maze and its two subsequent modifications, the final mastering of which was not completed until many weeks had passed. It is evident from the foregoing account that some more general disturbance of the processes by which learning is achieved is responsible for the poorer records made by these rats.

During the past fifteen years the importance of the old associational explanations of learning in the development of psychological theory has been steadily diminishing. Among the pioneers of this movement away from the simple machine theories of learning is the paper by Shepard and Fogelsonger (1913). In this study an ingenious series of experiments with nonsense syllables brings out in a variety of ways the necessity for a reënvisagement of the entire conception of the learning processes. The simple association theories would lead one to expect exactly the opposite of the results obtained. To the writer, the most important single result of Shepard's paper is the demonstration that not only the components of a stimulus situation but the pat-

tern in which it is presented determines the response. Where identically the same components of a stimulus situation were presented in the test as in the training series, but in the latter the pattern had been altered either spatially or temporally, the response when elicited showed a remarkable lengthening in reaction time and a decrease in accuracy. The tendency in psychology today is toward a recognition of the relationship existing between the total form of the stimulating situation and the adequacy of the response. Such a condition of affairs on the behavior side has as its counterpart on the neurological side the realization that the central nervous system does not work in the simple patterns such as we find represented in current psychological texts, and occasionally even in the periodicals. We must return to our own problem with this attitude in view.

Since it was destruction of a part of the cerebral cortex that resulted in the abnormalities of learning, retention, and adaptation to modifications, we naturally turn to a consideration of this cortex in seeking for some explanation of the phenomena observed. The structure of the cerebral cortex of even so simple a mammal as the rat is found to be such that its anatomical interconnections may be regarded, for all practical purposes, as infinite in number. The microscopic structure of the frontal portions presents a picture of cell-bodies among which are intertwined innumerable end-arborizations of other cells. Only some of the connections have ever been worked out satisfactorily, and these do not help us much in the problem that confronts us. Certain it is that some very remote nuclei send their axons in this direction; and if these do not themselves terminate in the frontal region, they at least make contacts with others that do. It is apparently unnecessary that a given area stand in the direct pathway of the main impulses for it to affect the ultimate behavior concerned. It is therefore probably also unnecessary that an injury involve the main tracts for it to disturb a piece of behavior. More especially does this seem to be the case when the process known as learning is concerned, in which a number of correlation centers is probably involved. We have found in our series of experiments that the production of lesions in the frontal regions,

even though slight in extent, not only disturbs redintegration of old habits but also makes original learning more difficult, and the mastering of modifications of already-learned patterns a longer process than would otherwise be the case. The results of this paper, then, would seem to indicate that the frontal region of cerebral cortex cannot be ignored in the study of learning and kindred processes, even though they be of a purely " kinaesthetic " nature, as some students of animal behavior would have us regard maze learning.

Is the disturbance that follows the operation due to an actual anatomical lack of specific fibers that had been used in the cortical pattern involved in a given maze habit? Or has the operation, in removing a part of the central nervous system, so altered the general activity of the whole cortex that when the habit is again called into play by the appropriate surroundings, the old neural organization will not function as it had done previous to the surgical interference? The answer is not easily given. And the riddle is not made the simpler when we consider that the group of animals operated upon before training of any kind exhibited the same sort of peculiarity in learning Maze II and its modifications as did the group that had previously been trained in it. In other words, group B which had nothing in the way of old maze habits to lose by the operations still experienced the same difficulty in the same sort of way when confronted with a maze problem to solve after the operations as did group A. Evidently any explanation that is offered must be applicable to the one case as well as to the other.

The architectonics of the cerebral cortex of the rat present an anatomical organization such as might form the basis for a closely integrated functional system. Physiological experiment points to a partial division of this system into different fields, each of which tends to dominate in some one function or group of related functions. Now since every cortical field is probably connected with every other cortical field (Herrick, 1926), we may look upon the whole cerebral cortex as a physiologically integrated system—not necessarily as an equipotential one, but as one in which neural activity may have far-reaching and perhaps

" total " effects within the cortex, *i.e.*, effects that involve all parts more or less, with certain components more active under one set of circumstances and others dominant under different ones. If we assume that at a given moment this functional system is in a state of physiological equilibrium and that with each change induced by new activities a new equilibrium must be reached, certain conclusions follow. Of course, the system is continually fluctuating; and whatever assumptions as to equilibria we make must take this fact into consideration. Thus, for simplicity's sake, our hypothetical account must be crude in the extreme in order to be intelligible at all.

Let us assume that when the portion of the frontal cortex was extirpated in our experiments there resulted a disturbance of the physiological equilibrium in that particular part of the cerebrum. That is to say, the functional configuration existing at that time within the little sub-system known as the frontal pole before the insertion of the knife has been disrupted. Now such a disturbance may have a great deal of effect upon the activity concerned or it may have little; but it seems safe to assume that *some* disturbance must result from such heroic treatment of so delicately balanced a system. A portion of this delicately adjusted system has suffered the destruction of its anatomical basis, or at least a separation from the rest. The local disturbance to the particular section actually involved in the lesion is obvious enough to be admitted at once without further exposition. But we have assumed for the whole cortical structure a closely integrated and balanced organization; and it is a physical fact that, given such a system, if we are to assume a balance at all then the disturbance of one little sub-section must call forth compensatory functional rearrangements in every other part of the system, until an equilibrium is again restored. But the new configuration is not the same as the old. It could not be. For must it not take into account a condition that was not at all present in the old one, namely, the loss of some of its basic structure? Now the animal is again faced with the same stimulus situation as before in the shape of an already-mastered temporal pattern of movements in a familiar maze. It goes almost without saying that the new

configuration necessitated by the surgical interference will not meet the demands made upon it as well as that of the normals will whose functional pattern, barring the effects of the lapse of time common to both, remains relatively the same.

If the functional disorganization has been slight, the effects may not be very obvious in a very simple problem. This seems to have been the case in the work of Lashley and Franz (1917) in which a simple two-choice situation comprised the whole of the problem (fig. 1). Even in maze patterns as complex as those used in our experiments the initial adjustments may be made just as well or nearly as well as with the normal animals, which indeed we found to be the case in our results. But when it comes to finishing off the task, overcoming the tendency to leave the correct path now and then to wander into one or several of the numerous cul-de-sacs that branch off from it, the new configuration does not seem adequate until a greater number of trials has been gone through. Were it simply a matter of establishing the same dynamic equilibrium as that already achieved by the normals, we should expect to find in the subsequent modifications of the Maze II habit which has itself to be mastered before the modifications of its pattern are attempted, a record on the part of the operated rats strictly comparable to that of their normal controls. For, since under this latter assumption they would have become adapted to Maze II by reaching the same identical functional configuration as that of the normals, they should start off with their next problem on the same basis as the normals. But we find on the contrary that in learning the modifications of Maze II they behave in a manner exactly similar to the way in which their adjustment to that maze itself was made after the operation. This is quite different from the way in which they adjusted to the problems before the operation and the way in which the normal controls adjusted to the same problems both before and after the retention period, during which these latter were not operated upon. The equilibrium from which the operated rats must start is fundamentally different from that of the normals because of the actual destruction of some of its anatomical components, which must have resulted in a disrup-

tion of the previous dynamic equilibrium. Just because of this, we are forced to conclude that the change in the functional configuration of neural patterns involved in the redintegration of an old habit and in the mastering of modifications of it must be not only more extensive than that of the normals, but also quite different.

The results obtained with the group that had not received training previous to the operations may be accounted for as well on the same assumptions. Here there is certainly no question of "cutting out" a maze habit! Members of this group had nothing in the way of maze habits to lose when they came up for the cerebral operations. We do find them in their very first problem, Maze II after the operation, making a poorer showing than that of the group which had been trained previously in this and other maze patterns before being operated upon. But when retention effects in the previously trained group are allowed for, the record made by the untrained group shows a striking similarity to that of the trained. In other words, although their absolute record is not so good, their mode of adjustment is very similar. In the subsequent modifications both groups do about as well, one excelling somewhat in the first change and the other to about the same degree in the second. If we were to assume that the cerebral cortex of these animals is physiologically equipotential, it would be difficult to account for the results in the untrained group. Rather they fit into the assumption that the operation in the case of the previously untrained, as in the case of the previously trained, has effected the disturbance of an equilibrated system; so that the subsequent learning necessitates the striking of a new balance in a manner different from that struck by the normal animals, and for some reason one that cannot be as efficiently reached. Thus the two phenomena turn out to be related as regards their physiological basis just as they are similar in their learning behavior.

Until the mechanisms underlying the formation, retention, and modification of habits have been worked out, it remains impossible to construct in detail a serviceable theory on the basis of the meager facts that this and previous experimental work have

brought to light. At the same time, progress not infrequently comes as a result of allowing theory to step a bit in advance of the known facts provided it be recognized at the time, and not subsequently forgotten, that the structure thus erected is only a scaffolding and not a permanent edifice. The suggestions that have been offered in the foregoing discussion must be regarded as purely tentative in nature; not so much settled convictions as conclusions arrived at through a study of the results obtained in these experiments, and influenced to some extent by the trend of current psychological and neurological theory.

VII. SUMMARY

Thirty-six rats were divided into four groups and given different training. Two groups were trained in one maze pattern, Maze I, and then in a modification of it, after which they were given an entirely new maze pattern to learn. This was followed by a three-week period of no-practice during which one of the groups suffered surgical destruction of part of the frontal cortex, while the other did not. Both groups were then returned to the maze pattern learned just before the operations, Maze II, for a retention test; and they were subsequently trained in two modifications of Maze II in order that their ability to adapt themselves to changes might be studied. The other two groups were given Maze II as their very first problem; one group had been operated upon before starting it, the other had not. These two groups were also trained subsequently in the two modifications of Maze II. Records were thus taken on 8,553 trials and the data presented in the form of tables and learning curves.

Work done by previous investigators with a simple two-choice apparatus gave results that were interpreted as indicating no connection between maze learning and the frontal regions of the cerebrum. Their findings were probably due to the simplicity of the apparatus, which does not allow a sufficient variety of errors for observers to gather data that would bring out fine differences in learning and retention. Even though disturbances in the learning and redintegration processes might have been present, the adjustments required of the animals were so simple and so rapidly completed as to render differences indiscernible to the experimenter. Even simple maze patterns of three or four cul-de-sacs would probably have given different results. The patterns and the succession of maze problems used in the experiments reported in this paper made it possible to demonstrate unmistakable differences between the learning behavior of rats with injury to frontal cortex and that of normal animals. The following results were obtained:

Rats with destruction of frontal cortex were able to learn entirely new problems in the maze; they showed a certain amount of retention of the effects of old maze habits after operation; and they were able to adapt to modifications of already-formed habits. *In all three activities,* however, *the operated upon groups were distinctly inferior to their normal controls.*

The most outstanding result of the operations was the contrast between initial trials and later learning. *The beginnings of the curves for both normal and abnormal groups are strictly comparable in contour; but the latter parts of the same curves are very different,* those of the normal controls rapidly reaching the base line and those of the operated rats continuing to zig-zag on for some distance. This difference is to be found in learning, in redintegration, and in adaptation to change; and it is as marked as it is consistent.

We are forced to conclude that cerebral destruction involving the frontal regions of the rat has a decided effect upon the learning, redintegration, and adaptation to modifications of the maze habit. The results of the experimental work seem to indicate that this effect is not due simply to the removal of specific cortical components. Rather we prefer to regard the cerebral operations as having disequilibrated an exceedingly complex dynamic system in such a manner that future adjustments cannot be made with the same ease as in the case of normal cortical equilibrium. The results for both those animals that had been trained before the operations and those that had not appear to be covered equally well by this theoretical assumption.

VIII. LIST OF REFERENCES CITED

BURNETT, THEODORE C. 1912. Some Observations on Decerebrate Frogs with Especial Reference to the Formation of Associations. *Amer. Jour. Physiol.*, vol. 30, pp. 80–87.

CAMERON, NORMAN. 1927. Individual Records of the Maze Learning of Albino Rats after Partial Decortication. Ann Arbor: University of Michigan Library. 75 pp.

CRAIGIE, E. HORNE. 1925. An Introduction to the Finer Anatomy of the Central Nervous System Based upon that of the Albino Rat. Philadelphia: P. Blakiston's Son and Company. 194 pp.

DONALDSON, HENRY H. 1924. The Rat: Data and Reference Tables for the Albino Rat (*Mus norvegicus albinus*) and the Norway Rat (*Mus norvegicus*). Philadelphia: Memoirs of the Wistar Institute of Anatomy and Biology, no. 6, 2d ed.

FRANZ, S. I., and LASHLEY, K. S. 1917. The Retention of Habits by the Rat after Destruction of the Frontal Portion of the Cerebrum. *Psychobiology*, vol. 1, pp. 3–19.

GREENMAN, M. J., and DUHRING, F. L. 1923. Breeding and Care of the Albino Rat for Research Purposes. Philadelphia: Wistar Institute of Anatomy and Biology.

HERRICK, C. JUDSON. 1924. Neurological Foundations of Animal Behavior. New York: Henry Holt and Company. xii+334 pp.

—— 1926. Brains of Rats and Men: A Survey of the Origin and Biological Significance of the Cerebral Cortex. Chicago: The University of Chicago Press. xiii+382 pp.

LASHLEY, K. S. 1920. Studies of Cerebral Function in Learning. I. *Psychobiology*, vol. 2, pp. 55–135.

LASHLEY, K. S., and FRANZ, S. I. 1917. The Effects of Cerebral Destruction upon Habit Formation and Retention in the Albino Rat. *Psychobiology*, vol. 1, pp. 71–139.

SHEPARD, JOHN F. 1921. Some Experiments on Learning. *Psychol. Bull.*, vol. 18, pp. 79–80.

SHEPARD, JOHN F., and FOGELSONGER, H. M. 1913. Studies in Association and Inhibition. *Psychol. Rev.*, vol. 20, pp. 290–311.

WARDEN, CARL J. 1925. The Value of the Preliminary Period of Feeding in the Problem Box. *Jour. Comp. Psychol.*, vol. 5, pp. 365–372.

WATSON, JOHN B. 1914. Behavior: An Introduction to Comparative Psychology. New York: Henry Holt and Company. xii+439 pp.

YERKES, ROBERT M. 1903. The Instincts, Habits, and Reactions of the Frog. Part I. The Associative Processes of the Green Frog. *Psychol. Monogr.*, vol. 4, pp. 579–597.